Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem

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ABSTRACT

To better understand the effects of fisheries and ocean productivity on the northeastern Ionian Sea we constructed an *Ecopath* with *Ecosim* model with 22 functional groups. Data on biomass, production/biomass, consumption/biomass, and diet for each group were estimated or extrapolated from the literature. Fisheries landings and discards were also included. Temporal trajectories were simulated using *Ecosim*. The model was fitted with time-series data for the most important groups from 1964 to 2006. Simulations highlighted a decline of top predators and of most of the commercial species since the late 1970s. The model shows that the decline of fish resources was mainly caused by an intensive fishing pressure that occurred in the area until the end of the 1990s and also by changes in primary production that impacted the trajectories of the main functional groups. In particular, simulated changes through time in *PP* impacted the abundance trends of all the commercial species, showing a cascade-up effect through the ecosystem. The application of *Ecopath* with *Ecosim* was a useful tool for understanding the trends of the main functional groups of the northeastern Ionian Sea. The model underlined that management actions are needed to restore and protect target species including marine mammals, pelagic and demersal fishes. In particular, measures to reduce overfishing, illegal fishing activities and to respect existing legislations are in need. Moreover, the adoption of marine protected areas could be an effective management measure to guarantee prey survival and to sustain marine predators.

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1. Introduction

Exploitation of marine resources has a long history in the Mediterranean Sea. Yet, fisheries research and management was only developed after World War II, particularly in the northwestern portion of the basin (Farrugio et al., 1993). Statistical reports of catches and effort are often unreliable, and actual takes are often underestimated (Briand, 2000). Commercially valuable species go directly to public markets and regional auctions, and this catch is often not included in the official records. Moreover, there is limited oversight and enforcement, especially with regard to illegal net and mesh size, landing and marketing of undersized fish, and compliance to restrictions on fishing season and areas (Farrugio et al., 1993; EC, 2003). While the fishing effort has been increasing over the past 50 years, Mediterranean catch rates have been declining over the last decade, possibly as a consequence of a 'fishing down the food web' effect (Grainger and Garcia, 1996; Pauly and Palomares, 2000; Stergiou and Koulouris, 2000) that occurs when higher trophic level predators are overfished and removed from the ecosystem, and gradually replaced by lower trophic level organisms. In the Hellenic Seas, the 'fishing down' effect has been observed in different areas of the Aegean Sea while it has been less pronounced in the Ionian Sea (Stergiou and Koulouris, 2000). In particular, as pointed out by Stergiou (2005), this phenomenon is less evident in areas where small pelagic fishes with low trophic level dominate the catches and their decline leads to an increase of the catches of fishes with higher trophic level.

In the northeastern Ionian Sea, evidence of overfishing has been observed since the mid 1980s (Papaconstantinou et al., 1988a; Papaconstantinou and Stergiou, 1995; Stergiou et al., 1997). This could be attributed to intensive fishing effort as observed throughout Greece and in particular in the Ionian Sea until the end of the 1990s (Kapadagakis et al., 2001; Stergiou et al., 2007a). Also, European Commission statistics indicate that trawl and purse seine catches have declined in the Hellenic Ionian Sea over the last decade suggesting a decline in pelagic and demersal stocks (EC, 2004).

Moreover, since the end of 1990s Bearzi et al. (2008a) observed a substantial decline of short-beaked common dolphin and an intensive exploitation of epipelagic fish stocks (major prey of this cetacean), suggesting that reduction in prey availability could be the potential cause of this decrease.

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In Greece, the legal framework to regulate fisheries issues has been outlined by the Fishing Code (Law Decree 420/70) since the early 1970s (Papaconstantinou, 2005). Yet, the existing legislation did not successfully prevent the overfishing of demersal and pelagic stocks, due to the inadequacy of the current fisheries management system (Stergiou et al., 1997, 2007a) as well as to illegal fishing practices.

Because of the complex dynamics of marine ecosystems and the difficulty of managing single species, fisheries management is gradually migrating away from single species assessments and toward an ecosystem-based approach (Pauly and Christensen, 1996; Pauly et al., 2002; Smith et al., 2007). As part of this approach, we used ecosystem modeling to investigate trophic interactions, direct and indirect impacts of local fisheries, and fisheries-related ecological perturbations. In particular, we investigated the temporal dynamics of the Ionian Sea food web from 1964 to 2003 using fishing pressure and environmental factors as main drivers and we explored ecosystem changes through time using ecosystem indicators.

2. Materials and methods

2.1. Study area

This study describes a marine ecosystem in the northeastern Ionian Sea, western Greece. The study area covers 1021 km^2 of sea surface; it includes the islands of Meganisi, Kalamos and Kastos and is delimited by the mainland of Greece, the island of Lefkada and the northern portions of Kefalonia and Ithaca (Fig. 1). The bottom includes seagrass meadows (*Posidonia oceanica* and *Cymodocea nodosa*), sand, and mud (silt-clay) in areas deeper than 50 m

(Haritonidis and Tsekos, 1976; Zenetos et al., 1997). A study conducted by Casotti et al. (2003) shows that this area is extremely oligotrophic. Values of Chlorophyll *a*, nutrients and particulate organic carbon were among the lowest found in Mediterranean coastal waters (Pitta et al., 1998).

The northeastern Ionian Sea is influenced by main water masses including the North Atlantic Water (NAW), Ionian Surface Water (ISW), Levantine Intermediate Water (LIW) and Deep Water (DW) of the eastern Mediterranean. The NAW consists mainly of water saturated in oxygen, low in salinity and poor in nutrients, extending from the surface to about 60 m. The ISW, as well as the NAW, extends from the surface to about 60 m, but it is saltier and warmer than the NAW and flows in the area only in the summer. (Malanotte-Rizzoli et al., 1998). The LIW occupies subsurface layers (80–150 m) and is characterized by higher salinities and nutrients, while the DW has colder and more uniform water that extends from the lower part of the LIW down to the bottom (Bousoulenga et al., 1990; Psyllidou-Giouranovits et al., 1994; Malanotte-Rizzoli et al., 1998; Ramfos et al., 2005). The oxygen and nutrient pattern of the northeastern Ionian Sea are also influenced by cyclonic and anticyclonic gyres (Souvermezoglou et al., 1992). Most of the study area is relatively shallow, ranging in depth between 100 and 200 m.

The marine fisheries landings of Greece have been recorded since 1964 by the National Statistical Service of Hellas (NSSH Bulletins, 1964–2003). Greek waters have been separated into 18 statistical fishing subareas (Fig. 2). The fishing area covered by this study corresponds to Area 4 and partially to Area 5 (Fig. 2). Commercial fisheries in the study area include bottom trawlers, purse seiners, beach seiners and artisanal boats operating longlines and trammel nets (Bearzi et al., 2008a). According to Tsikliras et al. (2007), about 70 species of fish, cephalopods and crustaceans are
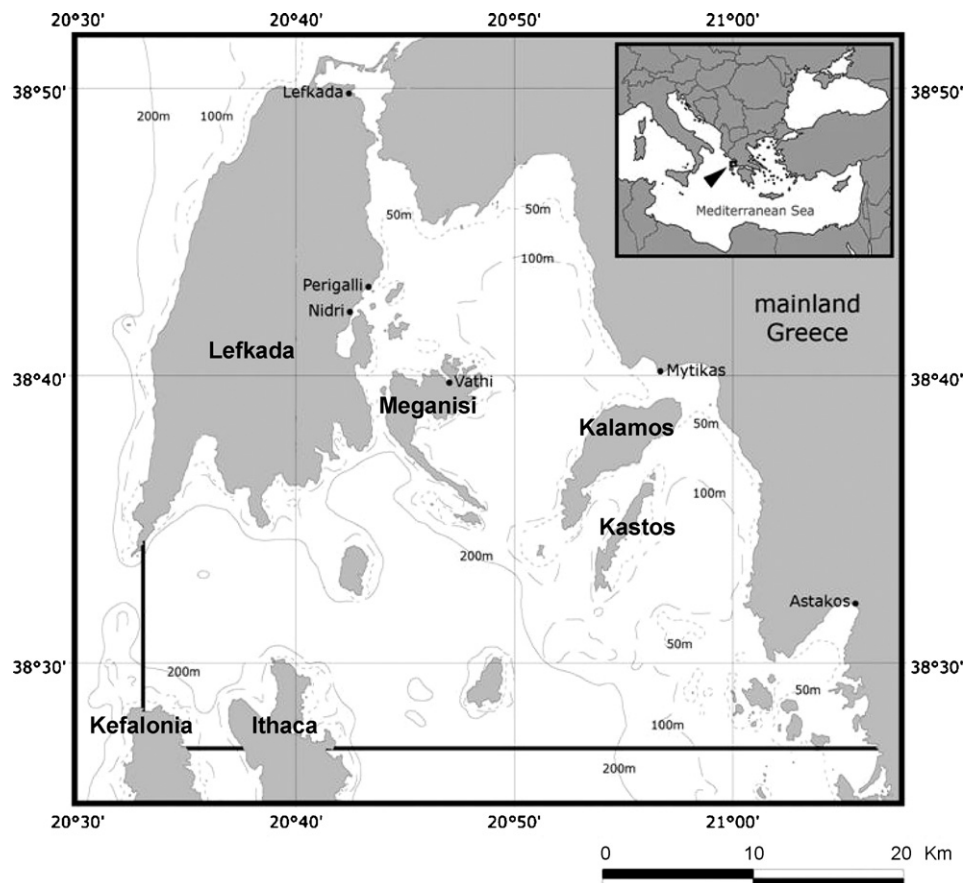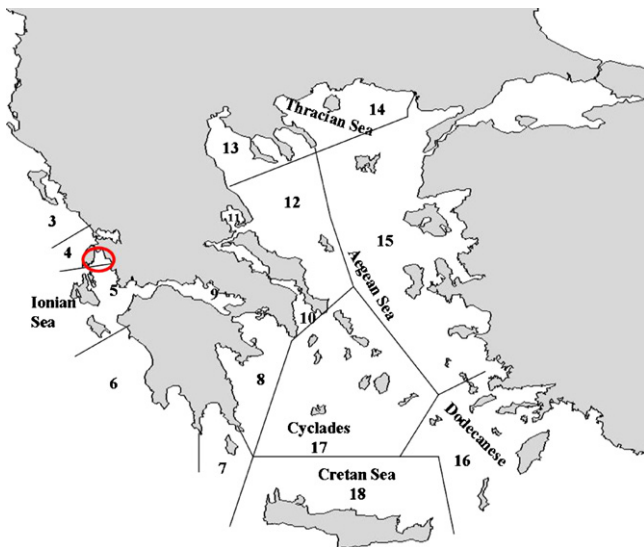

Fig. 1. The northeastern Ionian Sea. The study area is highlighted with a black border.

Fig. 2. The 18 Greek statistical fishing subareas. The mean total landings were taken from the subarea n.4 (red circle near the left edge). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

fished commercially in the area, with a few constituting the main targets: European pilchard (*Sardina pilchardus*); European anchovy (*Engraulis encrasicolus*); Mediterranean horse mackerel (*Trachurus mediterraneus*); Atlantic bonito (*Sarda sarda*); bogue (*Boops boops*); picarel (*Spicara smaris*); European hake (*Merluccius merluccius*); red mullet (*Mullus barbatus*) and striped red mullet (*Mullus surmuletus*).

2.2. The model

Ecopath with Ecosim is the most widely used ecosystem model and the number of studies that employ this model have increased exponentially in the last decade (Christensen and Walters, 2004). *Ecopath* was created by Polovina (1984) and subsequently further developed by Christensen and Pauly (1992) and Walters et al. (1997). It is a mass-balanced model that provides a static description of an ecosystem at a precise period in time (Walters et al., 1997). It can describe all the principal autotrophs and heterotrophs species individually or by aggregating them into functional groups (species with similar ecotrophic role) and incorporate data on biomass, consumption, production and efficiency; furthermore, fishing activities are included by adding data on landings, discards and by-catch as well as bio-economic parameters (i.e., value and cost).

2.2.1. Ecopath and the mass-balanced approach

The *Ecopath* model is based on two main equations. In the first one (see Eq. (1)), the biological production of a functional group is equal to the sum of fishing mortality, predation mortality, net migration, biomass accumulation, and other unexplained mortality

$$\left(\frac{P}{B}\right)_i B_i = Y_i + \sum_j B_j \left(\frac{Q}{B}\right)_j DC_{ji} + E_i + BA_i + \left(\frac{P}{B}\right)_i B_i (1 - EE_i) \quad (1)$$

where (P/B) is the production to biomass ratio for a certain functional group (i), B_i is the biomass of a group (i), Y_i the total fishery catch rate of group (i), $(Q/B)_j$ is the consumption to biomass ratio for each predator (j), DC_{ji} is the proportion of the group (i) in the diet of predator (j), E_i is the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate for the group (i), EE_i is the ecotrophic efficiency, and $(1 - EE_i)$ represents mortality other than predation and fishing. In the second equation (see Eq. (2)), the con-

sumption of a functional group is equal to the sum of production, respiration and unassimilated food.

$$consumption = production + respiration + unassimilated\,food \quad (2)$$

The implication of these two equations is that the model is mass-balanced; under this assumption, *Ecopath* uses and solves a system of linear equations (one for each functional group present in the system) estimating missing parameters (Christensen and Pauly, 1995; Christensen and Walters, 2004). Therefore, the input parameters (B, P/B, Q/B, and DC) are entered first, and then the mass-balance in the model is ensured. To do so, we used the manual mass-balanced procedure and we modified the model by adjusting the input parameters of those groups with $EE > 1$. In particular, we changed those parameters associated with higher uncertainty, i.e., diet matrix, P/B and to a lesser extent biomass (Christensen and Walters, 2004).

2.2.2. Model analysis

Trophic flows were quantified using *Ecopath*. Trophic flows in terms of total productions, consumptions, respirations, catches and flow to detritus were analysed to represent ecosystem structure and its exploitation. The total system throughput (TST), calculated as the sum of all these flows, was also given as indicator of the size of the entire ecosystem in term of flow (Christensen and Walters, 2004; Christensen et al., 2005). Moreover, the trophic level (*TL*) of each functional group was calculated using the following formula:

$$TL_j = 1 + \sum_{j=1}^{n} DC_{ji} TL_i \quad (3)$$

where j is the predator of prey i, DC_{ji} is the fraction of prey i in the diet of each predator j, and TL_i is the *TL* of prey i. By definition a *TL* of I is attributed to primary producers and detritus, *TL* of II to herbivores, *TL* of III to first order carnivores and *TL* of IV to second order carnivores. A flow diagram was created using Ecopath version 6 to better represent trophic flows and trophic levels of the northeastern Ionian Sea ecosystem.

We then used a pedigree routine to describe the origin and quality of the data in the model (Christensen and Walters, 2004; Christensen et al., 2005).

2.2.3. Ecosim and the fitting procedure

Ecosim provides temporal simulations using the initial parameters of the *Ecopath* master equation (Eq. (4)). It works with a couple of differential equations to estimate biomass fluxes as follows:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \quad (4)$$

where dB_i/dt is the biomass growth rate of group (i) during the interval dt, g_i is the net growth efficiency (production/consumption ratio), I_i is the immigration rate, M_i and F_i are natural and fishing mortality rates of group (i), e_i is emigration rate (Walters et al., 1997; Christensen et al., 2005; Pauly et al., 2000; Christensen and Walters, 2004). *Ecosim* describes the interactions between predators and prey by attributing a vulnerability term for each of these interactions. This vulnerability parameter sets the maximum increase in predation mortality a given predator can cause on a given prey. Low values of vulnerability (close to 1) mean that prey production determines the predation mortality (phenomenon also known as 'bottom-up' control) while high values of vulnerability (e.g., 100) mean that predator biomass determines how much prey is consumed (top-down control) (Christensen and Walters, 2004).

Ecosim was used to run dynamic simulations starting from the *Ecopath* model, incorporating time-series estimates (for the period

1964–2008) of biomass, by-catch, catch per unit effort (CPUE) and catches for those functional groups with available information. Time series of effort data (for the period 1964–2003) were used to drive the model. Each *Ecosim* scenario was fitted by adjusting prey vulnerability and by adding an environmental driver to the model to represent changes through time in nutrient concentration. *Ecosim* output scenarios were compared to observed time-series data to obtain a goodness of fit (Christensen et al., 2005). The fit that best represents the 'observed' data was chosen.

In detail, we first applied the 'fit to time series procedure' of *Ecosim*, to search for those vulnerability values that would minimize the sum of squared deviation (*SS*) of observed data from model predictions. We then, adjusted some of the default *Ecosim* parameters to further decrease the *SS* of certain functional groups. More precisely, the maximum relative feeding time was set to 10 for marine mammals and seabirds and to 2.0 (default value) for other functional groups, considering that if prey becomes more scarce, marine mammals and seabirds will spend more time looking for their food resources (Christensen et al., 2005). The feeding time adjustment rate was set to 0.5 for marine mammals and sea birds and to 0 for the other groups. This is because marine mammals and sea birds are more likely to change their search feeding time as food availability varies (Christensen et al., 2005). Fishing mortality can be expressed as the product of catchability and fishing effort, where catchability represents the proportion of the stock removed by a unit of fishing effort. By default, *Ecosim* considers the fishing effort (f_0) equal to fishing mortality (F_0), assuming a catchability (q_0) equal to 1, where f_0, F_0, and q_0 are the baseline fishing effort, fishing mortality rate, and catchability provided by *Ecopath*. The catchability may be a function of stock size and *Ecosim* has a density-dependent catchability effect (Q_{max}/q_0), setting the Q_{max}/q_0 ratio with a value greater than 1.0 (Christensen et al., 2005). In this study, we tried different values of density-dependent catchability for sardines and anchovies. The best fit was found when set to 6.0 and 3.0 for sardines and anchovies, respectively, since these small pelagic fishes school and so their catchability may remain high even when their abundance decreases. We also tried to change the density-dependent catchability for other pelagic schooling fish (e.g., tuna) but we did not observe any improvement in the fitting.

We also allowed for density-dependent predator–prey switching for common bottlenose dolphins and monk seals by changing the default value 0 (no density-dependent predator–prey switching) to 2 (maximum density-dependent predator–prey switching) to take into account the opportunistic foraging behaviour of these two marine mammal species, who can adapt their diet depending on prey availability (Panou et al., 1993, Bearzi et al., 2008b). We did not change these values for short-beaked common dolphins, seabirds, turtles and fishes since such mechanisms are considered less relevant (Bearzi et al., 2005, 2008a; Christensen et al., 2005).

Furthermore, to evaluate the impact of environmental factors on the marine organisms we used an automated procedure in *Ecosim* involving a forcing function applied to simulate a time series of nutrient loading within the ecosystem. This procedure allowed the estimation of changes in nutrient concentration, which impact the primary production rates for the producer groups. Nutrient anomalies change the total amount of energy that enters in the system allowing a cascading-up effect that increases or decreases food availability through the ecosystem (Preikshot, 2007). In our case, nutrient anomaly impacted directly the primary production biomass affecting therefore sardines and anchovies trends.

At the end, we also applied a 'trophic mediation function' to assess the possibility that changes in biomass of one organism may have no trophic effects on other functional groups. In *Ecosim*, trophic interaction rates are described as flow rates:

$$\text{flow rate} = \frac{a_{ij}^*}{A_{ij}V_{ij}P_j}$$

where a_{ij}^* is the "rate of effective search" parameter, A_{ij} the restricted area where predator j forages on prey i, V_{ij} vulnerable prey biomass and P_j the predator abundance. This equation recognizes that predators search for prey only over restricted foraging arenas and that the vulnerable prey biomass is distributed only over such areas (Christensen et al., 2005). In *Ecosim*, mediation functions are used to influence the flow rate of certain organism by altering:

- the area over which vulnerable prey/predators are distributed,
- the "rate of effective search" parameter, and
- the vulnerability exchange rate v_{ij} that determines the vulnerable prey biomass V_{ij}.

In our case, the mediation function was used to evaluate if the decline of short-beaked common dolphins have had any indirect effect (e.g., by increasing the feeding area A_{ij}) on the common bottlenose dolphin population. No correlations have been observed, however.

2.2.4. Ecosystem indicators

After the fitting procedure, we examined different ecosystem indicators to evaluate changes in structure and functioning of the northeastern Ionian Sea ecosystem (Christensen and Walters, 2004). In particular we selected the Kempton's index of biodiversity, an index that expresses biomass species diversity by considering those organisms with trophic levels 3 or higher (Kempton and Taylor, 1976; Ainsworth and Pitcher, 2006); the ratio between total demersal *versus* total pelagic biomass (*D/P* ratio) expected to increase with an increase in fishing pressure (Cury et al., 2005; Coll et al., 2008); the mean trophic level of the Ionian Sea community (mTLco) excluding those functional groups with *TL* = 1 and calculated as the weighted average of the *TL* of all the species within the ecosystem and the mean trophic level of the catches (mTLc) calculated as the weighted average of the *TL* of fisheries target species (Pauly et al., 1998).

2.3. The input parameters

An *Ecopath with Ecosim* model (software version 5) was constructed for the northeastern Ionian Sea for the baseline year of 1964. This year was chosen because of the information on catch time series that was available from 1964 to 2003. A total of 22 functional groups were considered in the model, including three marine mammal species, one sea turtle species, one sea bird, eight fishes, five invertebrates, and two primary producer groups. European hake, European pilchard, round sardinella (*Sardinella aurita*) and European anchovy as well as the three species of marine mammals were considered separately due to their importance in the trophic web. For each group, four input parameters were estimated: biomass, production per unit of biomass (*P/B*), consumption per unit of biomass (*Q/B*) and diet composition. The biomass of each functional group, expressed as t of wet weight per km^2, was obtained from field surveys or estimated from empirical equations of population reconstruction. The *P/B* and *Q/B* ratio were estimated using empirical equations (Allen, 1971; Pauly, 1980; Christensen et al., 2005) or were taken from literature and expressed as annual rates. A diet matrix was constructed using either field studies (e.g., stomach contents) or diet data obtained from the literature for the same species in similar ecosystems (Tables 1 and 2). For a detailed description of the functional groups, please refer to Appendix A.

Table 1
Functional groups and their basic modified *Ecopath* parameters with equations and references used for the northeastern Ionian Sea balanced model. Modified parameters are in italics.

Functional groups	Data	Equations	Source
1. *Short-beaked common dolphin* (*Delphinus delphis*)			
Mean body weight (kg)	68	From empirical equation: $W = 7.5814(L - 140)^{0.534}$	Kastelein et al. (2000)
Biomass (t/km²)	0.016	From a logist growth model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Christensen (2006)
Production/biomass (/year)	0.09	Life history table	Barlow and Boveng (1991)
Consumption/biomass (/year)	25.43	From modified energy requirement equation: $E = aW^{0.714}$	Perez et al. (1990); Hunter (2005)
2. *Common bottlenose dolphin* (*Tursiops truncatus*)			
Mean body weight (kg)	179	From empirical equation: $W = 17.261e^{0.0156(L - 100)}$	Kastelein et al. (2002)
Biomass (t/km²)	0.009		Interviews with fishers
Production/biomass (/year)	0.08	Life history table	Barlow and Boveng (1991)
Consumption/biomass (/year)	24.42	From modified energy requirement equation: $E = aW^{0.714}$	Perez et al. (1990); Hunter (2005)
3. *Monk seals* (*Monachus monachus*)			
Mean body weight (kg)	300		Boulva (1979); Marchessaux (1989)
Biomass (t/km²)	0.015	From a logist growth model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Christensen (2006)
Production/biomass (/year)	0.12	Life history table	Barlow and Boveng (1991)
Consumption/biomass (/year)	12.59	From modified energy requirement equation: $E = aW^{0.714}$	Perez et al. (1990); Hunter (2005)
4. *Sea birds* (*Calonetris diomedea; Larus cachinnans; Larus fuscus; Sterna nilotica; Sterna sandvicensis; Phalacrocorax carbo*)			
Biomass (t/km²)	0.0031		Personal communication by V. Karpouzi
Production/biomass (/year)	4.6		Pinnegar and Polunin (2004)
Consumption/biomass (/year)	105.43		Karpouzi et al. (2007)
5. *Sea turtles* (*Caretta caretta*)			
Mean body weight (kg)	68		EuroTurtle (2006)
Biomass (t/km²)	0.0069		Interviews with fishers
Production/biomass (/year)	0.19	Z = survival rate	Bjorndal et al. (2003); Mazaris et al. (2005); Casale et al. (2007)
Consumption/biomass (/year)	2.54		Coll et al. (2007)
6. *Tuna* (*Thunnus thynnus Katsuwonus pelamis, Euthynnus alletteratus*)			
Biomass (t/km²)	0.04		ICCAT (2003)
Production/biomass (/year)	0.2	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	ICCAT (2003); Froese and Pauly (2009)
Consumption/biomass (/year)	3.22	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^H$	Christensen et al. (2005)
7. *Swordfish* (*Xiphias gladius*)			
Biomass (t/km²)	0.06	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	*0.3*	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Megalofonou et al. (1987) and Froese and Pauly (2009)
Consumption/biomass (/year)	*4.6*	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^H$	Christensen et al. (2005)
8. *Sardines* (*Sardina pichardus, Sardinella aurita*)			
Biomass (t/km²)	2.1	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	*0.7*	Total mortality: $Z = K(L_{\infty} - L)/(L - L')$	Stergiou et al. (1997) and Froese and Pauly (2009)
Consumption/biomass (/year)	*8.68*	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^H$	Christensen et al. (2005)
9. *Anchovies* (*Engraulis encrasicolus*)			
Biomass (t/km²)	1.2	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	*0.8*	Total mortality: $Z = K(L_{\infty} - L)/(L - L')$	Stergiou et al. (1997) and Froese and Pauly (2009)
Consumption/biomass (/year)	*12.3*	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^H$	Christensen et al. (2005)
10. *Other pelagics* (*Dentex dentex; Diplodus annularis; Micromesistius poutassou; Mugil cephalus; Oblada melanura; Pagellus erythrinus; Pagrus pagrus; Sarda sarda; Sarpa salpa; Scomber japonicus; Scomber scombrus; Seriola dumerili; Spicara smaris; Spondyliosoma cantharus; Sprattus sprattus; Trachurus mediterraneus; Trachurus trachurus*)			
Biomass (t/km²)	1.95	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	*1.1*	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Papaconstantinou et al. (1988b); Papaconstantinou and Petrakis (1989); Stergiou et al. (1997); Stergiou and Moutopoulos (2001); Abaunza et al. (2003); Ragonese et al. (2004); Chilari et al. (2006); Zaboukas et al. (2006) and Froese and Pauly (2009)
Consumption/biomass (/year)	7.7	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^H$	
11. *Hake* (*Merluccius merluccius*)			
Biomass (t/km²)	0.18	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	*1.2*	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Papaconstantinou and Stergiou (1995)

Table 1 (*Continued*)

Functional groups	Data	Equations	Source
Consumption/biomass (/year)	3.46	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^{H}$	Papaconstantinou and Stergiou (1995)
12. *Other demersals* (*Boops boops*; *Lepidotrigla cavillone*; *Conger conger*; *Dicentrarchus labrax*; *Diplodus sargus sargus*; *Epinephelus marginatus*; *Helicolenus dactylopterus dactylopterus*; *Lophius piscatorius*; *Mullus barbatus*; *Mullus surmuletus*; *Polyprion americanus*; *Psetta maxima*; *Raya clavata*; *Solea solea*; *Sparus aurata*; Scorpaenidae and Serranidae)			
Biomass (t/km²)	0.9	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/Biomass (/year)	1.35	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Tsimenides and Ondrias (1980); Papaconstantinou et al. (1988a); Stergiou et al. (1997); Stergiou and Moutopoulos (2001) and Froese and Pauly (2009)
Consumption/biomass (/year)	7.43	$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^{H}$	
13. *Cephalopods* (Loliginidae and Ommastrepidae families; *Sepia officinalis*; *Octopus vulgaris* and other members of the family Octopodidae)			
Biomass (t/km²)	0.4	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	3.3	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Rodhouse and Nigmatullin (1996); Guerra (1979); Rodhouse and Nigmatullin (1996) and from Cephbase (www.cephbase.org)
Consumption/biomass (/year)	7.0	From daily feeding rate equation: $FR = 0.0683 + 0.0474W$	
14. *Crustaceans* (*Hommarus gammarus*; *Penaeus kerathurus*; *Carcinus aestuarii*; *Nephrops norvegicus* and miscellaneous small crustaceans)			
Biomass (t/km²)	*3.0*	Population reconstruction model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	Tsikliras et al. (2007)
Production/biomass (/year)	1.35	Total mortality: $Z = F + M$, where M = empirical equation (Pauly, 1980)	Abelló et al. (2001, 2002); Conides et al. (2006)
Consumption/biomass (/year)	6.5		Cartes and Maynou (1998); Maynou and Cartes (1998)
15. *Benthic invertebrates*			
Biomass (t/km²)	28.39	Converted to wet weight following Cauffope and Heymans (2005)	Zenetos (1993)
Production/biomass (/year)	2.5		Brey (2001)
Consumption/biomass (/year)	22.0		Brey (2001)
16. *Zooplankton*			
Biomass (t/km²)	3.7	Converted to wet weight following Cauffope and Heymans (2005)	Siokou-Frangou and Papathanassiou (1989); Panayotidis et al. (1994); Ramfos et al. (2006) Christou (1991)
Production/biomass (/year)	*18.0*		Pinnegar and Polunin (2004)
Consumption/biomass (/year)	40.0		
17. *Phytoplankton*			
Biomass (t/km²)	2.33		Pagou and Gotsis-Skretas (1990)
Production/biomass (/year)	*285.26*		Institute for Environment & Sustainability, EU Joint Research Center, Ispra, Italy
18. *Discards*			
Biomass (t/km²)	0.135		Machias et al. (2001); Tsimenides et al. (1995); Stergiou et al. (1996); Tzanatos et al. (2007)

2.3.1. Fisheries parameters

Fisheries information was obtained from direct observations conducted in 2007 by the Tethys Research Institute in the study area and from estimated parameters for the entire Greece (Stergiou et al., 2007a; Tsikliras et al., 2007; Bearzi et al., 2008a). A total of 308 fishing boats were observed of which 12 were purse seiners, 9 were bottom trawlers, 24 were beach seiners, 50 were longliners, and 213 trammel net boats (Bearzi et al., 2008a). The mean annual landings for the year 2007, were 1167 t year^{-1} for purse seiners, 529 t year^{-1} for beach seiners and 798 t year^{-1} for bottom trawlers (Bearzi et al., 2008a). The species composition of the mean landings per fishery was taken from Bearzi et al. (2008a) and from Stergiou et al. (2007a).
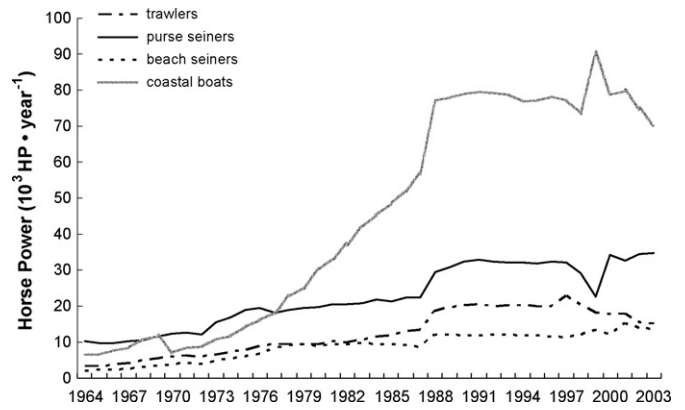
In order to consider landings from different boat sizes, trammel nets and longline fleets were split into two categories, small boats between 4 and 7 m, and large boats of 7+ meters (Bearzi et al., 2008a). We assumed one fisher per boat for the small boats and two fishers for the large boats. Based on these assumptions, the mean total landings for the coastal boats was 1078 t year^{-1} (Bearzi et al., 2008a). The mean estimated landing/fisher ratio was 3.48 t year^{-1} per person. This result is consistent with the value obtained by Stergiou et al. (2007a) for the whole of Greece, where the landings/fisher ratio for coastal boats was 3.42 t year^{-1} per per-

son. The fisheries landings for the year 2007 show that purse seiners catch the most with 32.7% of the total catch, followed by trammel netters 25.6%, trawlers 22.3%, beach seiners 14.8%, and longliners 4.6% (Bearzi et al., 2008a). The same percentage was used for the year 1964 with the mean total landings estimated by Tsikliras et al. (2007) (Table 3).

The mean total landings for the period 1964–2003 were taken from the Greek statistical fishing subarea #4 (Fig. 2). The mean total landings of this subarea included the study area as well as the Amvrakikos Gulf—a semi-closed shallow and eutrophic gulf situated north of the study area. In order to separate the landings of these two different ecosystems, we eliminated from the reported landings, species that occurred mainly in brackish waters based on information from *Fishbase* (Froese and Pauly, 2009). Secondly, we assumed that until 1990, in Amvrakikos, species like European pilchard, caramote prawn, red mullet and white seabream represented 40% of total landings of subarea 4, while European seabass and gilthead seabream was 10%, and all other marine species 5%. After 1990, a severe depletion has occurred for the target species (European pilchard, caramote prawn, and red mullet), constituting, therefore, only 10% of total catches; the main part of landings consisted of European seabass, gilthead seabream and white seabream with 40% (D. Moutopoulos, pers. comm.).

Table 2
Functional groups and their diet matrix for the northeastern Ionian Sea balanced model. Modified parameters are in italics.

Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Common d.																
2 Bottlenose d.																
3 Monk seal																
4 Sea birds																
5 Sea turtle																
6 Tuna																
7 Swordfish																
8 Sardine	0.50	0.02		0.25		0.24	0.28			0.01	0.21	8×10^{-3}	2×10^{-3}			
9 Anchovy	0.30	0.07		0.09		0.13	0.14			0.01	0.15	6×10^{-3}	6×10^{-3}			
10 Other pelagics	0.10	0.05	0.20	0.05		0.40	0.36			0.02	0.13	9×10^{-3}	3×10^{-3}			
11 Hake		0.44	0.45				2×10^{-4}									
12 Other demersals	0.05	0.39	0.10	7×10^{-3}			0.01				0.07	8×10^{-3}	4×10^{-3}	8×10^{-4}		
13 Cephalopod	0.05	0.03		0.03		0.07	0.10				0.04	0.06	4×10^{-3}	4×10^{-3}		
14 Crustacean		3×10^{-3}		0.07	0.04	0.15	0.12			4×10^{-3}	0.08	0.36	0.44	0.05		
15 Benthic inv.					0.52						0.32	0.54	0.56	0.58	6×10^{-3}	
16 Zooplankton					0.17			0.80	1.0	0.52				0.36	0.06	
17 Phytoplankton								0.20		0.44					10^{-5}	
18 Discards				0.20	0.19									10^{-5}		0.10
19 Detritus					0.07							5×10^{-3}			0.94	0.90
20 Import				0.31												
21 Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Fig. 3. Fishing effort (10^3 HP year^{-1}) for trawlers, purse seiners beach seiners and coastal boats.

Data on discards was taken from the literature (Tsimenides et al., 1995; Stergiou et al., 1996; Machias et al., 2001; Tzanatos et al., 2007) and the same percentage was used for the year 1964 (Table 4).

Fishing effort was not available for the study area; therefore, we extrapolated a time series fishing effort expressed as horse power (HP year^{-1}) for each type of fishery, using data from the Ionian Sea from Kapadagakis et al. (2001) for the period 1996–2000, and from Stergiou et al. (2007a) for Greece for the period 1964–1995 and 2001–2003. The resulting trends are shown in Fig. 3.

3. Results

3.1. Flow diagram, quality of the data and summary statistics

We used *Ecopath 6* to graphically represent trophic flows and trophic levels of the northeastern Ionian Sea ecosystem (Fig. 4). Functional groups are illustrated by their trophic levels (*TL*) ranging from 1 to 4.41, with highest values for common bottlenose dolphins, monk seals, swordfish, tuna and short-beaked common dolphins (*TL* > 4). All other fish groups have a *TL* between 3.7 (hake) and 3.09 (other pelagics) with the exception of sardines (*TL* = 2.89) that show a lower trophic level due to phytoplankton in their diet. Sea turtles, zooplankton and benthic invertebrates are classified between 2.8 and 2.0. Each functional group is represented as a circle and its size is proportional to its biomass in Fig. 4.

The pedigree index (0.497) for the model falls in the same range (0.4–0.599) as found by Morissette (2007) when comparing 50 balanced *Ecopath* models.

Statistics and flows quantified by *Ecopath* are reported in Table 5. The total system throughput and the total biomass (excluding detritus) were quite similar to another oligotrophic ecosystem model (Catalan Sea) analysed by Coll et al. in 2006. In both models the values were small compared to other ecosystems of high productivity (Coll et al., 2006b; Heymans et al., 2004). The mean trophic level of the catches was low because of small pelagic fishes with *TL* between 2.89 and 3.1 that dominate the catches of the northeastern Ionian Sea (Stergiou and Koulouris, 2000). The ratio between total primary production (*PP*) and total respiration (*R*) was high indicating that there was more energy produced than respired. Moreover, the primary production/biomass ratio (*PP/B*) was also high showing a low level of biomass accumulation compared with primary production. The system exhibited low rates of connectance and system omnivory index. These ecological indicators suggest, under Odum's theory (Odum, 1985), that the northeastern Ionian Sea ecosystem is at early developmental stage.

Table 3
Catches (t/km^2) by gear type and by functional group included in the *Ecopath* balanced model.

Functional groups	Purse seiners	Trawlers	Beach seiners	Small artisanals	Big artisanals
Tuna	3×10^{-3}			9×10^{-5}	7×10^{-4}
Swordfish				5×10^{-4}	6×10^{-3}
Sardine	0.06		0.03	4×10^{-3}	0.01
Anchovy	0.09		0.03	5×10^{-3}	0.02
Other pelagics	0.12	0.04	0.05	0.06	0.13
Hake		0.02	6×10^{-4}		
Other demersals	0.02	0.03	0.01	0.01	0.08
Cephalopod	0.01	0.02	5×10^{-3}	5×10^{-3}	0.01
Crustacean		0.01			
Sum	0.3458	0.1175	0.1181	0.0851	0.2511

Table 4
Discards (t/km^2) by gear type and by functional group included in the *Ecopath* balanced model.

Functional groups	Purse seiners	Trawlers	Beach seiners	Small artisanals	Big artisanals
Sea turtle					2.5×10^{-4}
Tuna					
Swordfish					
Sardine	0.011	6.6×10^{-3}		1×10^{-3}	3×10^{-3}
Anchovy	5×10^{-4}	0.018			
Other pelagics	0.036	9.9×10^{-3}	0.024	3×10^{-3}	0.01
Hake		3.5×10^{-4}		6.5×10^{-4}	2×10^{-3}
Other demersals	1.3×10^{-3}	8.8×10^{-3}	0.016	3×10^{-3}	9.5×10^{-3}
Cephalopod		1.3×10^{-3}			8×10^{-4}
Crustacean		8.5×10^{-4}		2.8×10^{-4}	
Benthic inv.					
Sum	0.0484	0.0458	0.0402	0.0087	0.0258

3.2. System productivity (nutrient forcing function)

Changes in nutrient concentration found by *Ecosim* are shown in Fig. 5. This trend has been compared with the trajectory of primary production (*PP*), from the year 1964 to the year 2006, estimated by *Ecosim* at the end of the fitting. Primary production rates for phytoplankton reacted differently to variation in nutrient concentration during each simulation. The generated trend of primary production showed low variation of *PP* through time, except for the years 1991–1994 and, to less extent 1996–1999 and 2003–2005, where high peaks were observed.

3.3. Time-series fitting and ecosystem indicators

Time-series fits are presented for the most important functional groups of this marine ecosystem (Fig. 6). The model reflected the rapid decline of short-beaked common dolphins and even with few data points also of monk seals when fishing pressure was used as main driver. However, the model was unable to predict the common bottlenose dolphin abundance trend for the period 1997–2008. No evidence was found to support the hypothesis that the decline of short-beaked common dolphins had benefited common bottlenose dolphins. We tried, indeed, to incorporate a
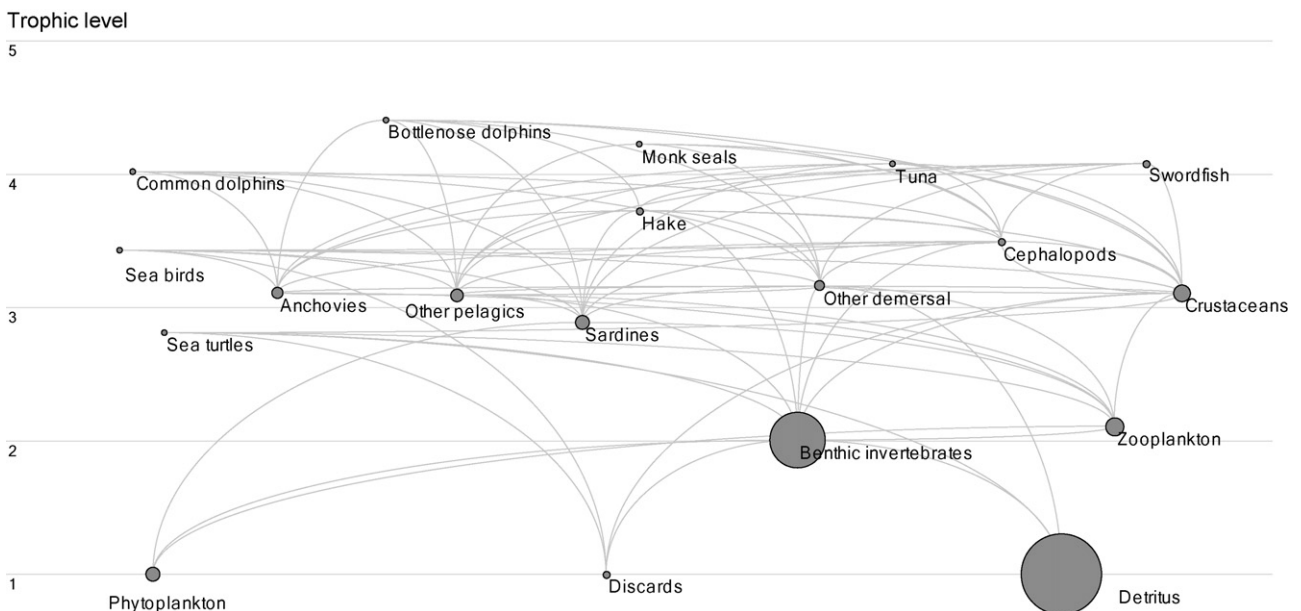

Fig. 4. Flow diagram of the northeastern Ionian Sea ecosystem. Each functional group is shown as a circle and its size is approximately proportional to its biomass. The trophic links between functional groups are also presented.

Table 5
Summary statistics of the northeastern Ionian Sea *Ecopath* model.

| Statistics	
Sum of all consumption	851.9 t/km^2/year
Sum of all exports	162.1 t/km^2/year
Sum of all respiratory flows	503.3 t/km^2/year
Sum of all flows into detritus	748.8 t/km^2/year
Total system throughput	2266.1 t/km^2/year
Sum of all production	813.6 t/km^2/year
Mean trophic level of the catch	3.1
Gross efficiency (catch/net p.p.)	0.002
Total net primary production	664.9 t/km^2/year
Total primary production/total respiration	1.3
Net system production	161.6 t/km^2/year
Total primary production/total biomass	15.0
Total biomass/total throughput	0.02
Total biomass (excluding detritus)	44.3 t/km^2/year
Total catches	1.1 t/km^2/year
Connectance Index	0.22
System Omnivory Index	0.1
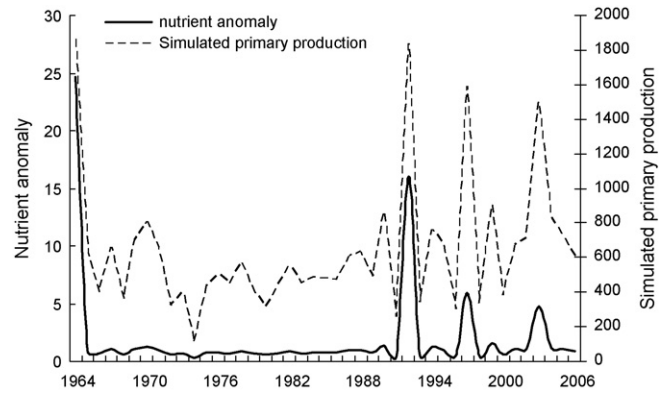
Fig. 5. Simulated nutrient anomaly for the northeastern Ionian Sea ecosystem, and modelled primary production (t km^{-2} year^{-1}) estimated by *Ecosim*.

mediation function in the model assuming that short-beaked common dolphins decline would have increased the feeding area of common bottlenose dolphins.

For sardine and anchovy CPUE from 1964 to 2003, the fishing effort was able to explain part of their decline. The best fit was found when fishing pressure and simulated changes in nutrient concentration within the ecosystem were considered jointly in the model (Fig. 6). Fig. 7 shows the sardine CPUE fit using fishing effort as driver (Fig. 7a) and using fishing effort and changes in nutrient concentration together (Fig. 7b).

Ecosim failed to reproduce the tuna CPUE trend. Several vulnerabilities and density-dependent catchabilities were tested in the
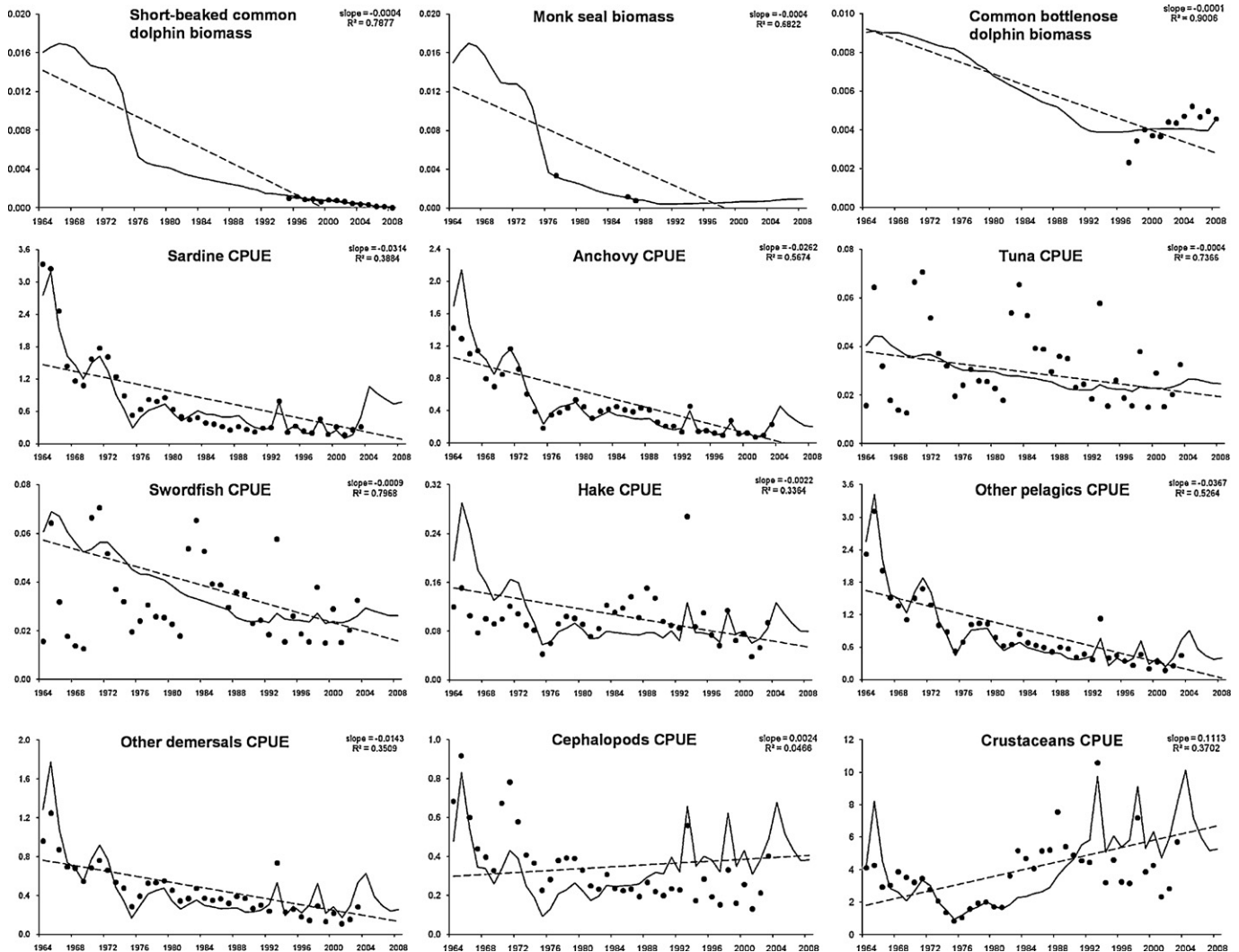
Fig. 6. Time series fitting between predicted (line) and observed biomass and CPUE values (dots) (t km^{-2}) for the period 1964–2008 using fishing effort and nutrient anomalies as main drivers. The estimated trends (thin line) are shown with the value of the slope and the coefficient of variation (R^2) for the regression model.
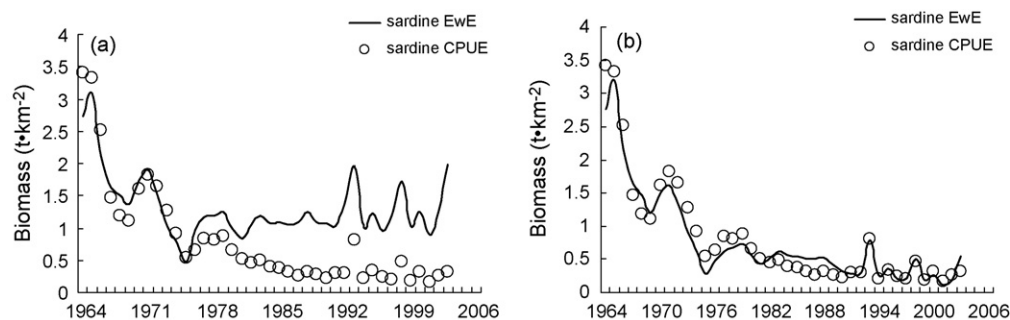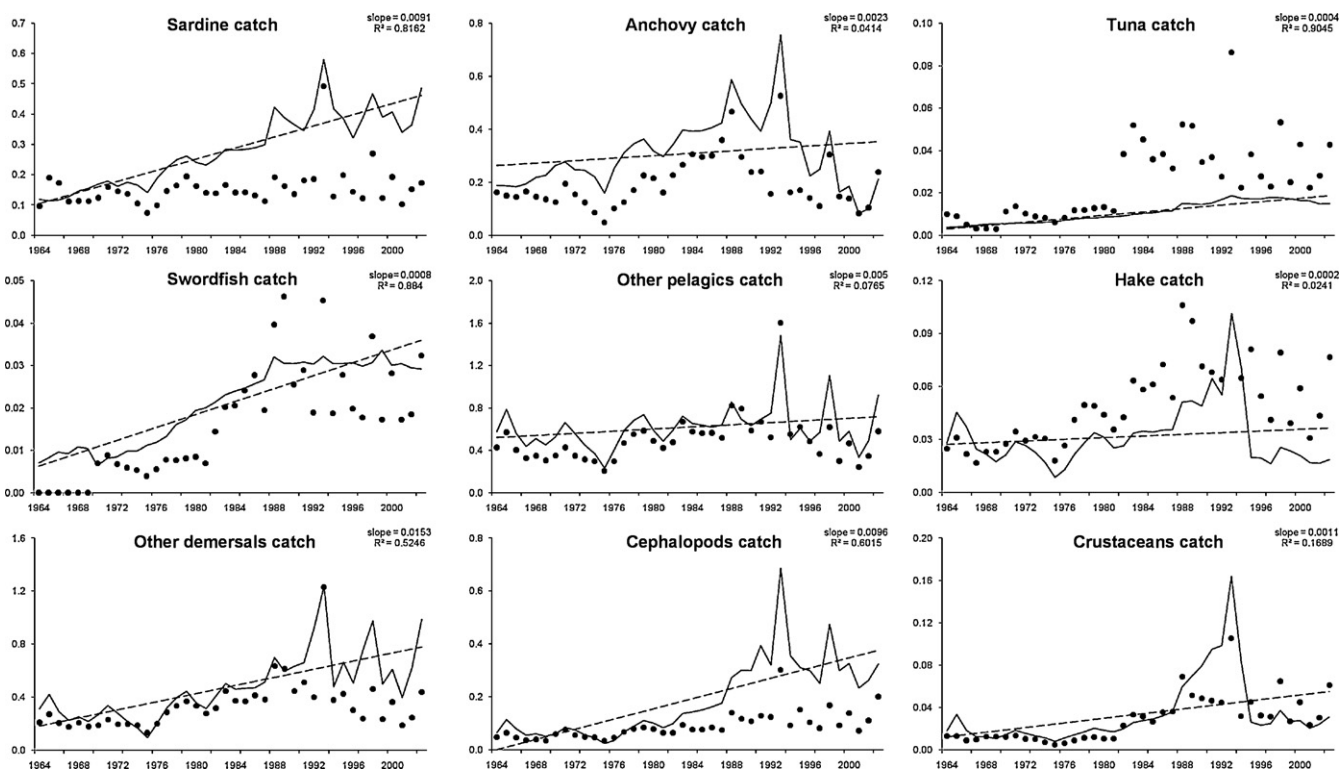
Fig. 7. Time series fitting between predicted (line) and observed catch data (t km⁻²) (dots) for the period 1964–2003 using fishing effort and nutrient anomalies as main drivers. The estimated trends (thin line) are shown with the value of the slope and the coefficient of variation (R^2) for the regression model.

model, but none of them were able to represent the fluctuations shown by tuna in the area. This is likely because the tuna dynamics are influenced by events at a much larger scale than represented here. A similar scenario was observed for the swordfish CPUE trend; the model was not able to reflect the annual fluctuations of the species in the area. However, a more defined trajectory may suggest that this stock has decreased since 1970.

The model replicated the changes in hake CPUE quite well, especially for the period 1968–1982, while it was not capable of following the trajectories for 1964–1981 and 1983–2003. The simulated changes in biomass for other pelagics and other demersals fitted the observed CPUE trends. This was done by searching for vulnerabilities and nutrients anomalies that would minimize the summed squared residuals between logged observed and predicted estimates. The model reflected the decline of these groups of fish since 1964. The modelled biomass trends for cephalopods and crustaceans had similarities with the observed CPUE changes, particularly between 1964 and 1982; however, Ecosim was not able to

find a good fit for the following years. In the crustaceans trend, even without a good match, the model seemed to capture the increase in CPUE from the year 1983 onwards.

The predicted sardine landings and to a lesser extent the anchovy and cephalopod landings showed higher values compared to the observed. The model was not able to fit tuna, hake and swordfish catches, probably due to the bad fit observed in CPUE trajectories; in particular tuna and hake catches were underestimated by Ecosim predictions. Regarding the other functional groups, other pelagics, other demersals and crustaceans, the simulations did fit the observed trends relatively well (Fig. 8).

The ecosystem indicators showed evident changes through time in the structure of the northeastern Ionian Sea ecosystem. In particular, the Kempton's biodiversity index as well as the mean trophic level of the community (mTLco, for those organisms with $TL > 1$) showed a clear decrease from 1964 to 2003 while the demersal/pelagic biomass ratio and the mean trophic level of the catches (mTLc) significantly increased (Fig. 9).

Fig. 8. Time series fitting between predicted sardine biomass and estimated sardine CPUE, from 1964 to 2003, without and with the nutrient loading forcing function.
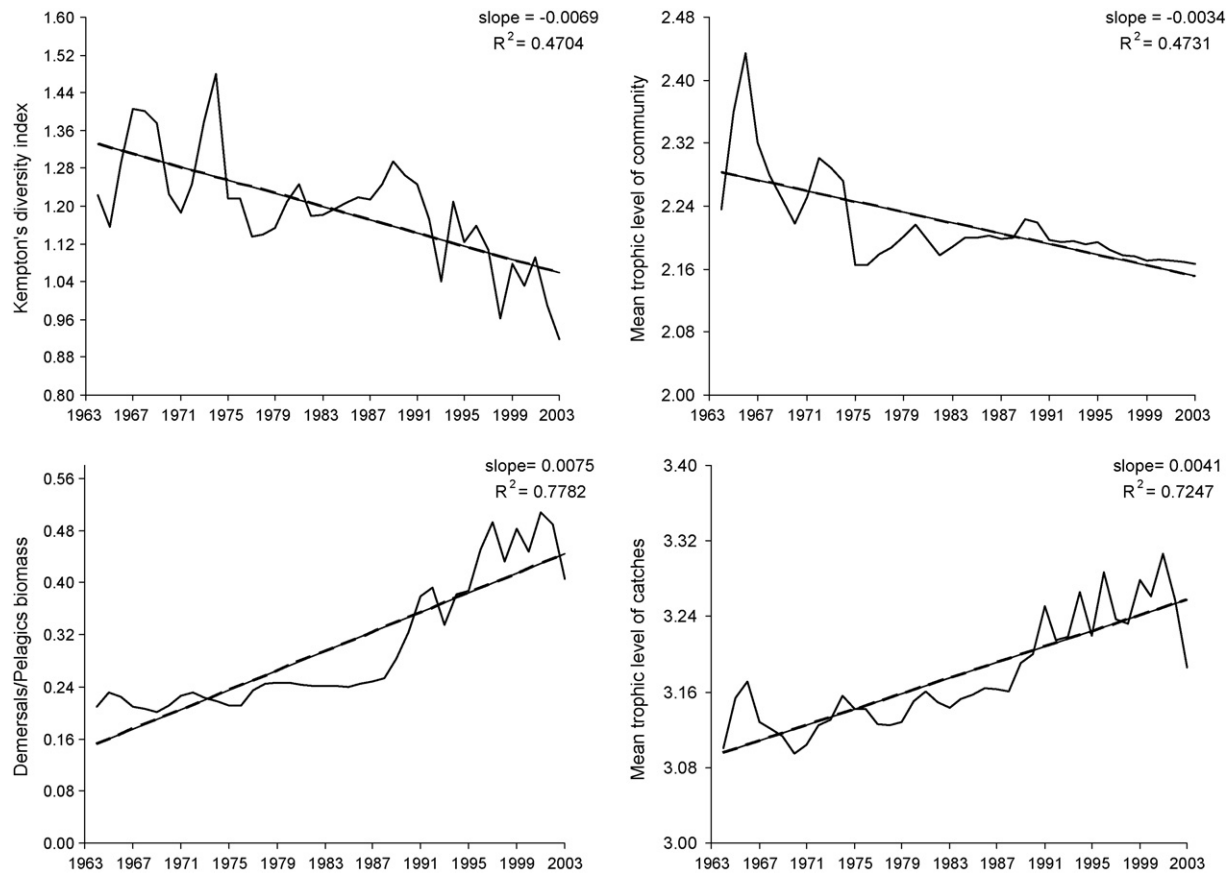
Fig. 9. Ecosystem indicators calculated from *Ecosim* model for the period 1964–2003. The estimated trends (thin line) are shown with the value of the slope and the coefficient of variation (R^2) for the regression model.

4. Discussion

4.1. Time-series fitting

Ecopath with Ecosim was used for the Northeastern Ionian Sea to better understand the trophic interactions of the main functional groups in the study area, and, in particular, to assess the impact of local fisheries on the marine fauna. Results seem to support the hypothesis that the observed decline of short-beaked common dolphins was due to overfishing of epipelagic fishes (Bearzi et al., 2006, 2008a). In particular, the model suggested that this decline continued after the 1970s at a slower rate as a consequence of the decline of sardines and anchovies stocks, the main prey items of short-beaked common dolphins. It is likely that by-catch of dolphins has added to the decline, but there are only few records of by-catch reported in the area (Bearzi, 2006). Moreover, surveys conducted outside the study area, have recorded no migration or a change in spatial distribution of these photoidentified dolphins, suggesting that the population has not moved elsewhere (Bearzi et al., 2005). Therefore, reduction in prey availability appeared to be the most plausible reason for the observed decrease of short-beaked common dolphin numbers in the area.

Simulated catches of sardines and anchovies have increased through time, reaching a peak in 1993 and declining afterwards (Fig. 8). An interesting aspect of the scenarios in Fig. 8 is that predicted sardine landings and in part also anchovy landings showed stronger decline than the reported landings. While there may be several reasons for this difference, an interesting one is that it may suggest an underestimation of the catch data. This agrees with other studies that have pointed out that Greek landing data are unreliable (Stergiou et al., 1997, 1998; Briand, 2000) and fishers may deliber-

ately misreport their catches to avoid stricter regulations or higher taxation (Bearzi et al., 2006). No significant results were obtained for other large marine predators, such as tuna and swordfish, feeding on epipelagic prey (sardines and anchovies). The model was unable to capture their biomass trend most probably because these pelagic fishes are highly migratory and influenced by events at a scale much larger than studied here.

Even if we had only few data points to validate the trajectory of monk seal biomass, the model was capable of reproducing it well, suggesting that direct and incidental killings caused by fishers and to a lesser extent intensive fishing pressure were the main cause of the decline of monk seal biomass. In Greece, for the past 40 years, fishers have killed seals as competitors for fish resources. In particular, deliberate killing and by-catch in fishing gear are a likely cause of population decline in the Ionian Sea (Cebrian and Vlachoutsikou, 1992; Panou et al., 1993; Androukaki et al., 1999).

The model was unable to reproduce observed abundance for the common bottlenose dolphin. This maybe due to the fact that trophic interactions were not responsible for the trajectory. For most of the commercial fish stocks the model was able to follow the observed trends. In particular, the biomasses of sardines, anchovies, pelagic and demersal fishes have shown a remarkable decline since the late 1960s. The predicted collapse was mainly caused by an intensive fishing effort that increased until the end of the 1990s, as observed also in the literature (Kapadagakis et al., 2001; Stergiou et al., 2007a). The simulated trajectories shown by the model concord with other studies for the eastern Ionian Sea that demonstrated how trawl and purse seine catches have declined considerably between 1996 and 2000, suggesting a decline in both pelagic and demersal stocks (EC, 2004; Stergiou et al., 2007b). Another interesting aspect of these scenarios is that, while most important pelagic
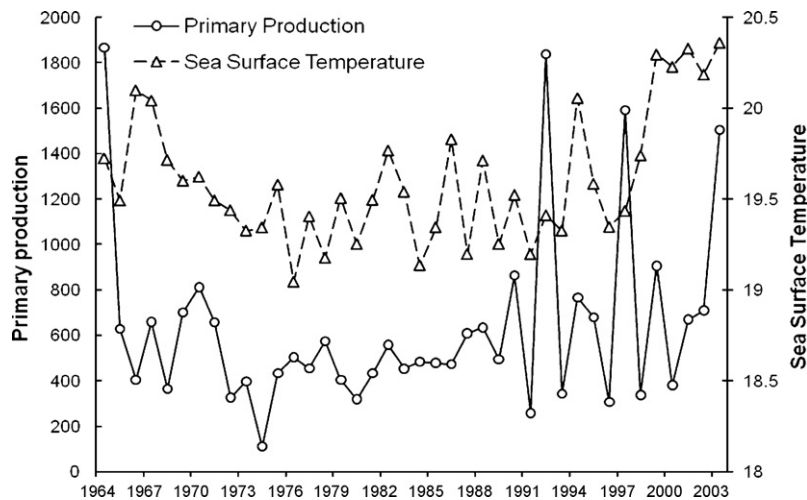
Fig. 10. Comparison between the sea surface temperature (°C) time series of the northeastern Ionian Sea with the primary production estimated by *Ecosim* for the 1964–2003 period.

and demersal stocks have clearly decreased through time, crustaceans CPUE has gradually increased. This may be related to a cascading effect caused by predation release.

Another important step that allowed the predicted trends of sardines, anchovies, pelagic and demersal CPUE to be fitted with the observed trajectories was obtained when changes of nutrient concentration were added to the model. Changes through time in nutrient loading have consequently generated changes in primary production (*PP*) (Fig. 5). The simulated trend of primary production has evidenced a generally lower variation of *PP* through time with the exception of three high peaks observed for the periods 1991–1994, 1996–1999 and 2003–2005. It was not possible to compare this predicted *PP* trajectory with observations because of a lack of data from the study area.

The modelled trend could be related to observed environmental shifts that have influenced the thermohaline circulation of the Eastern Ionian Sea. Several studies have indicated changes in water mass features of the South Aegean Sea between 1986 and 1997 that have affected the Eastern Ionian Sea circulation (Theocharis et al., 1992; Stergiou et al., 1997; Theocharis et al., 1999; Manca et al., 2002). According to these studies, since 1990, waters from the Cretan Sea were found for the first time in the deep and bottom water of the Ionian Sea. The mechanisms that have induced these hydrological changes were mainly due to two different forcing factors in two distinct periods inside the Cretan Sea. The first one was related to an increase of salinity, between 1987 and 1992, due to a continuous period of reduced rainfall, while the second corresponded to a decrease of temperature between 1992 and 1994 (Theocharis et al., 1992, 1999). The combinations of these two factors created a mass of dense water and a strong continuous outflow towards deep parts of the Ionian Sea. This phenomenon has changed the hydrological structure of the Eastern Mediterranean bringing warm, saline, and very dense waters rich in oxygen into the Ionian Sea (Stergiou et al., 1997; Theocharis et al., 1999). Manca et al. (2002) have demonstrated that these climatic shifts have modified the dynamics of the upper, intermediate and bottom layers of the Ionian Sea also in the period 1997–1999. In particular, the upper layer was mainly influenced by a warmer and less saline water mass, the intermediate layer had higher values of salinity and waters richer in oxygen, and the bottom layer was influenced by denser waters of Aegean origin.

To assess if the simulated primary production trajectory was affected by changes in temperature, we compared the trend in temperature of the study area with the *PP* trajectory from the period 1964–2003. The sea surface temperature (°C) time-series dataset

(Fig. 10) was obtained using the NOAA sea surface temperature database (http://nomads.ncdc.noaa.gov). The obtained temperature trend was correlated with the simulated *PP* trajectory using the Spearman's rank correlation test. The results of this analysis showed a positive correlation between the two variables with a rho = 0.36 and *p*-value = 0.010. This outcome supports the hypothesis that hydrological changes may have affected the primary production of the study area.

Simulated temporal trajectories highlighted a clear decline of marine mammals and commercially important species due to overfishing, direct and indirect killings and changes in ocean productivity. The model suggest that target species like sardines, anchovies, other pelagics and demersals were overexploited since the late 1970s; this was mainly attributed to unregulated fishing pressure that occurred until the end of 1990s and to illegal activities. Moreover, it also seemed that the level of primary production played an important role in the trajectories of the main functional groups. In particular, simulated changes through time in *PP* concentration impacted the abundance trends of all the commercial species, showing a cascade-up effect through the ecosystem.

Furthermore, ecosystem indicators analysed by the model have also shown clear changes in the structure of the northeastern Ionian Sea from 1964 to 2003 (Fig. 9). Both the Kempton's biodiversity index (for those organisms with $TL \geq 3$) and the mean trophic level of the community (excluding $TL = 1$), have shown a consistent decline through time in their trends supporting the decrease of high trophic level organisms (e.g., marine mammals) and the increase of lower trophic level groups (e.g., cephalopods, crustaceans, benthic invertebrates). On the other hand, the demersal/pelagic biomass ratio has increased linearly with time, reflecting the decline of small pelagic fish biomass, particularly sardines which are the main target of the local fisheries, and a consequent increase of demersal species. The mean trophic level of the catches has also increased through time supporting the decrease of sardine and anchovy stocks and the increase of fishes having higher trophic level. These results agree with the study of Stergiou (2005) that showed how in Hellenic waters, between 1980 and 2000, the mean trophic level of the catch increased due to an increase in the catches of fishes having trophic levels 3.5–4, and with the outcomes of another Mediterranean ecosystem model (Catalan Sea) where the pelagic food web has progressively shifted to a food web mainly dominated by demersal organisms (Coll et al., 2008).

These results have clearly highlighted the deterioration of the northeastern Ionian Sea ecosystem mainly due to intensive overex-

ploitation of marine resources and to changes in ocean productivity. The model has underlined that management actions are essential for the restoration and protection of the species that inhabit this marine ecosystem. In particular, measures to reduce overfishing, illegal fishing activities and to respect existing legislations are in need. Moreover, the adoption of a marine protected area (MPA) seems to be an effective management measure to enhance prey survival and to sustain marine predators (Stergiou et al., 1997, 2007a; Bearzi et al., 2006). The creation of MPAs could be particularly successful in coastal areas like the northeastern Ionian Sea where the extreme multi-species and multi-gear nature of the inshore fisheries make their management difficult (Stergiou et al., 1997).

Appendix A.

A.1. Short-beaked common dolphins and common bottlenose dolphins

Short-beaked common dolphin and common bottlenose dolphin abundance time series were available, respectively, for years 1995–2007 and 1997–2008. In 1995, the estimated number of short-beaked common dolphins was 127. However, their population showed a steady decline until 2007 (Bearzi et al., 2006, 2008a). Common bottlenose dolphins have shown a low density in the area and relatively stable trends (Bearzi et al., 2006); in 1997, the estimated number of common bottlenose dolphins was 26 (Tethys, unpublished data).

The biomass of short-beaked common dolphin for the year 1964 was calculated using the population reconstruction developed by Christensen (2006). The equation is a logistic growth model (Eq. (A.1)):

$$N_{t+1} = N_t + rN_t \left(\frac{1 - N_t}{k} \right) - C_t \tag{A.1}$$

where r is the intrinsic rate of growth, N_t is the abundance at the time t, k is the carrying capacity and C_t is the by-catch. In particular, for C_t, different values were tested to obtain an N_t sequence that better fit the observed abundance. One run was done by setting the by-catch value equal to 1, a second run with a value equal to 3 and a final run with the value of 6. The intrinsic rate parameter r (0.09 year^{-1}) was estimated using a life history table model from Barlow and Boveng (1991). The best carrying capacity (k) estimate for the year 1964 found by the model was 240 individuals with a by-catch of 6 individuals per year.

Mean body weight was determined according to the empirical equation of Kastelein et al. (2000) (Eq. (A.2)):

$$W = 7.5814(L - 140)^{0.534} \tag{A.2}$$

where W is the weight in kg and L is the standard body length in cm. Length was extracted from an Italian Stranding Data Bank (http://mammiferimarini.unipv.it/) due to unavailable data for Greece.

Common bottlenose dolphins biomass for the year 1964 was based on interviews with fishers that we conducted in 2006, following a similar approach conducted by Ainsworth (2004) and by Sáenz-Arroyo et al. (2005). We gathered qualitative information on population abundance changes, fisheries interactions, and spatial movements. Marine mammal pictures were shown to each interviewee. In particular, the questions were focused on whether the abundance of common bottlenose dolphins had increased, remained the same, or decreased during their fishing career. To quantify the trend, we asked if the number of common bottlenose dolphins were two times more in 1960s than 2006, the same in both years or two times less than 2006. Almost all the interviewees agreed that the population of common bottlenose dolphins in the 1960s was double the abundance of the year 2006.

Mean body weight was determined according to the empirical equation of Kastelein et al. (2002) (Eq. (A.3)):

$$W = 17.261e^{0.0156(L-100)} \tag{A.3}$$

Length was extracted from an Italian Stranding Data Bank using strandings of common bottlenose dolphins in the northern Ionian Sea.

The P/B for both species of dolphins was assumed to be equal to M (natural mortality), and it was calculated through a life history table model (Barlow and Boveng, 1991) that estimates survivorship and mortality according to the longevity of a given species. P/B of short-beaked common dolphins was subsequently modified to 0.05 year^{-1} to improve the fit with the observed data. Consumption per unit of biomass was found by using an empirical equation applied by Perez et al. (1990) to describe energy requirement (Eq. (A.4)):

$$E = aW^{0.75} \tag{A.4}$$

where E is the energy requirement per day (kcal day^{-1}), W the mean body weight (kg) and a is a coefficient varying with the group of mammals (a = 320 for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). The coefficient of 0.75, as often used in general for mammals, was subsequently changed to 0.714 following Hunter (2005) who estimated a more precise coefficient for marine mammals. The energy requirement of short-beaked common dolphins and common bottlenose dolphins was divided by the average prey caloric content (respectively 1361.4 and 1074.73 kcal per kg of prey).

Short-beaked common dolphin diet composition was obtained from stomach contents in the study area and in other neritic ecosystems, from fish scale sampling during surface feeding activities in the study area and from direct observation on feeding behaviour in the study area and in other Mediterranean coastal waters. The diet of the adult population is mainly dominated by sardines (50%), anchovies (30%), other pelagics (10%) such as blue whiting and *Trachurus* species, other demersals (5%) such as gobies, and cephalopods (5%) (Bearzi et al., 2008a). Information on common bottlenose dolphin diet was taken from the literature (Blanco et al., 2001). The common bottlenose dolphin diet is mainly composed of hake (43.9%), other demersals (38.5%) pelagics (5.1%), sardines (2.4%), anchovies (6.7%), cephalopods (3.1%) and crustaceans (0.3%). Few events of by-catch were documented for both species by Bearzi (2006) and included in the time series.

A.2. Mediterranean monk seal

The Mediterranean monk seal population in the Northeastern Ionian Sea is at a low density (Panou et al., 1993). Data on popula-

tion assessment were available for the years 1977, 1986 and 1987 (Goedicke, 1981; Panou et al., 1993). The biomass for 1964 was calculated using the population reconstruction model (Eq. (A.1)). The result suggests that approximately 50 individuals were inhabiting the area in that period of time. The average prey caloric content for the monk seal consumption was 1134.35 kcal per kg of prey. Mediterranean monk seal feeds opportunistically on a large number of prey (Jacobs and Panou, 1988; Cebrian et al., 1990; Scoullos et al., 1994; Boutiba and Abdelghani, 1997; Salman et al., 2001). In the model, we assumed a diet composed of demersal fish (45%), pelagic fish (20%), cephalopods (25%) and crustaceans (10%). Between 1963 and 1989, by-catch events were observed in the study area (Cebrian and Vlachoutsikou, 1992; Panou et al., 1993) and incorporated in the time series.

A.3. Seabirds

Unfortunately no publications were available for seabirds in the Northeastern Ionian Sea; therefore, data on population estimates, mortality and consumption rates were taken from similar ecosystems or from direct observations. Diet composition was taken from the literature (Fasola et al., 1989; Fasola and Bogliani, 1990; Bogliani et al., 1992; Grieco, 1994; Oro, 1996; Granadeiro et al., 1998). In particular, seabirds were assumed to feed on sardines (30%), anchovies (30%), other pelagics (5%), other demersals (4%), cephalopods (5%), crustaceans (2%), discards (15%) and terrestrial prey (9%). Data have been modified to satisfy mass balance in the model.

A.4. Loggerhead turtle

Little is known about abundance estimates, survival and consumption rates for the loggerhead turtle in the Mediterranean Sea. For the purposes of this study, we calculated the sea turtle biomass from the number of nests found in Kefalonia (Margaritoulis et al., 2003), following the criteria applied by the Turtle Expert Working Group (1998). The resulting biomass value is underestimated, as other nesting sites are likely present in the study area. On average, loggerhead adult females reproduce every 2.5 years (Richardson and Richardson, 1982; Hays, 2000; Broderick et al., 2002). On each migration, they make an average of 3.5 nests (Margaritoulis et al., 2003) and deposit approximately 100 eggs per nest (Turtle Expert Working Group, 1998). To estimate the population number of loggerhead turtles, the number of observed nests was divided by 3.5 nests/season (in this case 2.5 years) to obtain the number of adult females that nest every season. To calculate the biomass we assumed a 1:1 male to female ratio (Turtle Expert Working Group, 1998). The 1964 biomass was determined using the same methodology applied for common bottlenose dolphins, i.e., multiplying by a factor of 2 the biomass of 1996. Loggerhead turtle diet was assumed to be composed of crustaceans (4%), benthic invertebrates (52%), zooplankton (17%), discards (19%) and detritus (7%) (Houghton et al., 2000; Tomás et al., 2001; Revelles et al., 2007).

A.5. Tuna

The main Greek fisheries that target tuna are purse seiners and longliners. Little is known about tuna catch composition and fishing effort in Greece (ICCAT, 2003, 2005). Reported landings of bluefin tuna in the Northeastern Ionian Sea start in 1970, with an estimate of 9.9 t. Skipjack tuna and little tunny are caught with respectively 2.21 t (1964) and 0.08 t (1970) (Tsikliras et al., 2007). Biomass has been obtained from a stock assessment done by ICCAT for the area of Greece (ICCAT, 2003). The total biomass was calculated as 0.04 t km^{-2}. For the fishing mortality F, we used an average value estimated by ICCAT (2003) while natural mortality M was

calculated through the empirical model of Pauly (1980) (Eq. (A.5)):

$$M = K^{0.65} L_\infty^{-0.279} T_c^{0.463} \tag{A.5}$$

where M is the natural mortality (year^{-1}), K is the curvature parameter of the von Bertalanffy Growth Function (VBGF) (year^{-1}), L_∞ is the asymptotic length (cm) and T_c is the mean water temperature (°C). The P/B was 0.2 year^{-1}.

Q/B (3.22 year^{-1}) was determined according to the empirical equation of Christensen et al. (2005) (Eq. (A.6)):

$$\frac{Q}{B} = 10^{6.37} \times 0.0313^{Tk} \times W_\infty^{-0.168} \times 1.38^{Pf} \times 1.89^{Hd} \tag{A.6}$$

where W_∞ is the asymptotic body weight in grams, Tk is the mean annual temperature expressed as $1000/T$ ((°C) + 273.1), Pf equals 1 for predators and zooplankton feeders and 0 for all the others and Hd equals 1 for herbivores and 0 for carnivores.

All the required parameters used in these two equations were obtained from *Fishbase* (Froese and Pauly, 1995). The diet of tuna has been determined through literature information (Orsi-Relini et al., 1998; Stergiou and Karpouzi, 2002; Froese and Pauly, 2009): it principally consists of sardines (20%), anchovies (30%), other pelagics such as European sprat, bluefish and Atlantic mackerel (10%), cephalopods (25%) and crustaceans (15%). Input parameters were modified to balance the model.

A.6. Swordfish

The commercial species of swordfish in the study area is the *Xiphias gladius*. The Greek swordfish fishery developed in the early 1970s (De Metrio et al., 1988) and now extends from the Eastern Ionian Sea to the Levantine Sea. The main fishing gear used to catch swordfish is the longline. The fishing season starts in February and closes in September (Tserpes et al., 2006). The first reported catch for the study area was in 1970 with 0.007 t km^{-2} (Tsikliras et al., 2007).

The 1964 biomass was calculated from a population reconstruction model. The total mortality used was 0.38 year^{-1} (from Megalofonou et al., 1987, for the year 1986–1987); this value was then reduced to 0.30 year^{-1} to take into account variations of fishing mortality for the year 1964 and to fit the model to time-series data. Swordfish feeds mainly on sardines (19%), anchovies (46%), other pelagics such as European sprat, mackerels and seabreams (9%), hake (1%), other demersal species such as bogue (1%), cephalopods (17%) and crustaceans (7%) (Peristeraki and Tserpes, 2001; Stergiou and Karpouzi, 2002; Salman, 2004; Peristeraki et al., 2005). Diet input data were changed to balance the model.

A.7. Sardines

The species of sardines considered in this model are European pilchard and round sardinella. The first is one of the most important small-sized pelagic fish of Greece, mostly harvested for human consumption; the second is mainly used in the canning industry or as a bait for other pelagic fisheries targeting bluefin tuna and swordfish (Voulgaridou and Stergiou, 2003; Tsikliras et al., 2005).

Sardines dominate the mean total reported landings of Greece with 14.1% for the period 1989–2003. They are mainly caught by purse seiners, constituting 25.6% of their total catch, beach seiners with 11.7% and artisanal fisheries with 9.2% (Stergiou et al., 2007a). In the Northeastern Ionian Sea the mean total catch for the year 1964 was 0.19 t km^{-2} (Tsikliras et al., 2007). P/B was calculated using the following equation (Beverton and Holt, 1957) (Eq. (A.7)):

$$Z = K \frac{L_\infty - L}{L - L'} \tag{A.7}$$

where L_∞ is the asymptotic length, K is the VBGF curvature parameter, L is the mean length in the population, and L' represents the mean length at entry into the fishery. Required values were taken from Stergiou et al. (1997) and *Fishbase* (Froese and Pauly, 2009). P/B was 1.55 year^{-1}, calculated using data from 1983 to 1984; it was subsequently decreased to 0.7 year^{-1} for 1964 to better fit the biomass curve. Q/B was 9.84 year^{-1} and slightly decreased to balance the model. Sardine diet is mainly composed of zooplankton (80%) and phytoplankton (20%) (Stergiou and Karpouzi, 2002; Cunha et al., 2005; Somarakis et al., 2006).

A.8. Anchovy

European anchovy is a commercially important fisheries target in the Mediterranean basin. For the period 1989–2003, the European anchovy constitutes 14.6% of Greek landings, mainly caught by purse seine with 32.7% of the total catch, and in a smaller proportion by small scale artisanal fishery with only 4% of the total catch (Stergiou et al., 2007a). In the northeastern Ionian Sea the mean total catch for the year 1964 was 0.13 t km^{-2} (Tsikliras et al., 2007). Parameters to calculate P/B were obtained from *Fishbase* and Stergiou et al. (1997). This value was decreased to 0.8 year^{-1} to better fit the biomass trends. Consumption over biomass was 11.66 year^{-1}. It was modified successively to balance the model. Zooplankton is the only prey (100%) of European anchovies (Tudela and Palomera, 1995; Stergiou and Karpouzi, 2002).

A.9. Other pelagics

This group includes a variety of commercial pelagic species, among these, flathead mullet, chub mackerel, picarel and Mediterranean horse mackerel dominated the fisheries catches with respectively 2.4%, 4.2%, 5.6% and 6.4% of the total catch for the period 1982–2003 (Stergiou et al., 2007a). (Papaconstantinou, 1986; Stergiou and Papaconstantinou, 1987; Tsikliras et al., 2007).

In 1964 the mean reported landing was 0.39 t km^{-2} (Tsikliras et al., 2007). P/B was estimated by taking into account the different mortalities of these pelagic fish. It was then modified to balance the model. These parameters were estimated from the literature (Papaconstantinou et al., 1988b; Papaconstantinou and Petrakis, 1989; Stergiou et al., 1997; Stergiou and Moutopoulos, 2001; Abaunza et al., 2003; Ragonese et al., 2004; Chilari et al., 2006; Zaboukas et al., 2006) and from *Fishbase* (Froese and Pauly, 2009). The diet of other pelagics was mainly extrapolated from the literature (Daan, 1989; Papaconstantinou and Caragitsou, 1989; Gonçalves and Erzini, 1998; Ticina et al., 2000; Stergiou and Karpouzi, 2002; Olaso et al., 2005). We assumed 5% sardines, 5% anchovies, 5% other pelagics, 5% other demersals, 49% benthic invertebrates and 35% zooplankton. This diet has been adjusted to balance the model.

A.10. Hake

The European hake is a very common and commercially important demersal fish that inhabits the Greek seas (Vassilopoulou and Papaconstantinou, 1988; Papaconstantinou and Stergiou, 1995). In Greece, European hake represents 3.5% of the mean total landings; trawling is the main fishery, landing 10% of the total catch (Stergiou et al., 2007a). In 1964 the total landing of the Northeastern Ionian Sea was 0.022 t km^{-2} (Tsikliras et al., 2007). Stock biomass was available for the period 1994–1999 (Orsi-Relini et al., 2002). Diet is mostly composed of sardines (22%), anchovies (15%), other pelagics (13%) such as *S. smaris* and *Trachurus* sp., other demersals (7%) such as *Callionymus maculates* and gurnard *Lepidotrigla cavillone*, cephalopods (4%), crustaceans (8%) benthic invertebrates (32%) (Papaconstantinou and Caragitsou, 1987).

A.11. Other demersals

This group includes the major commercial demersal species caught in Greece (Papaconstantinou, 1986; Tsikliras et al., 2007).

Among the many species, red mullet and bogue dominated the fisheries catches during 1982–2003 with respectively 2.1% and 7.0% of the total catch (Stergiou et al., 2007a). In 1964, in the Northeastern Ionian Sea, the mean reported landing for this group was 0.15 t km^{-2} (Tsikliras et al., 2007). Diet was mainly extrapolated from the literature (Papaconstantinou and Caragitsou, 1989; Papaconstantinou et al., 1989; Labropoulou and Papadopoulou-Smith, 1999; Stergiou and Karpouzi, 2002). We assumed 1% sardines, 1% anchovies, 4% other pelagics, 2% other demersals, 10% crustaceans, 80% benthic invertebrates, 1% zooplankton and 1% detritus. This diet was adjusted to balance the model.

A.12. Cephalopods

This group considered most of the commercial cephalopods caught in Greece. In 1964 the mean reported catch was 0.017 t km^{-2} (Tsikliras et al., 2007).

Biomass information was available for the years 1999 and 2000 (Lefkaditou et al., 2003; Politou et al., 2003). Q/B was calculated using the daily feeding rate equation used by Rodhouse and Nigmatullin (1996) (Eq. (A.8)):

$$FR = 0.0683 + 0.0474W \tag{A.8}$$

where FR (g day^{-1}) is the feeding rate and W is the body mass. The parameters were taken from the literature (Guerra, 1979; Rodhouse and Nigmatullin, 1996) and from *Cephbase* (www.cephbase.org). Cephalopods feed mostly on sardines (20%), anchovies (10%), other pelagics (5%), other demersals (6%), cephalopods (3%), crustaceans (6%) and benthic invertebrates (50%) (Rodhouse and Nigmatullin, 1996; *Cephbase*). This diet was adjusted to balance the model.

A.13. Crustaceans

The main commercial crustaceans considered in the model were taken from Tsikliras et al. (2007). The mean reported landing for the year 1964, for the Northeastern Ionian Sea was 0.011 t km^{-2} (Tsikliras et al., 2007). Data on biomass was available for the year 2000 (D'Onghia et al., 2003; Politou et al., 2003). The total mortality was an average value of all the Z values found for each species of crustaceans (Abelló et al., 2001, 2002; Conides et al., 2006). The diet was composed of other demersals (5%), cephalopods (1%), crustaceans (12%), benthic invertebrates (80%), zooplankton (1%) and discards (1%) (Cartes, 1995; Sardà and Cartes, 1997; Cartes and Maynou, 1998; Maynou and Cartes, 1998; Kapiris, 2004). Diets were adjusted to balance the model.

A.14. Benthic invertebrates

This group considered a variety of organisms, including polychaetes, molluscs, echinoderms and other minor benthic groups. Values of dry weight biomass were obtained from Zenetos (1993). The mean annual biomass was converted to wet weight following Cauffope and Heymans (2005). The diet of this group consists of zooplankton (0.6%), phytoplankton (5%), discards (0.001%) and detritus (94%) (Brey, 2001).

A.15. Zooplankton

Copepods, cladocerans, appendicularians and chaetognats are the most abundant groups of zooplankton in the Northeastern Ionian Sea, with an abundance that decreases with depth between

50 and 200 m (Moraitou-Apostolopoulou and Vournazou, 1978; Rottini and Fabris, 1978; Pagou et al., 1989; Stergiou et al., 1997; Siokou-Frangou et al., 2005; Ramfos et al., 2006). Estimates of dry weight biomass were available for the year 2000, 1998, 1988, 1987 (Siokou-Frangou and Papathanassiou, 1989; Panayotidis et al., 1994; Ramfos et al., 2006). The 1987 estimate was taken as representative for the model; we transformed this value to wet weight following the conversion factors in Cauffope and Heymans (2005). P/B was estimated using zooplankton production found by Christou (1991); this value was subsequently reduced to balance the model. For Q/B no data was available for the eastern Ionian Sea, so we took a mean value used for model in Corsica (Pinnegar and Polunin, 2004). The diet consists of phytoplankton (90%) and zooplankton (10%) (Coll et al., 2007).

A.16. Phytoplankton

The productivity of the Northeastern Ionian Sea is very low and phytoplankton abundance in this area is among the lowest in Greece (Pagou et al., 1989; Pagou and Gotsis-Skretas, 1990; Gotsis-Skretas et al., 1993; Panayotidis et al., 1994; Stergiou et al., 1997; Pitta et al., 1998). Dinoflagellates, in particular *Gymnodium* sp., are the main species that can be found in these coastal waters, especially in summer and spring (Pagou et al., 1989; Pagou and Gotsis-Skretas, 1990; Gotsis-Skretas et al., 1993; Stergiou et al., 1997). An abundance estimate of 6220 cells/l was obtained from Pagou and Gotsis-Skretas (1990); this value was converted into $2.33 \, t \, km^{-2}$. The mean primary production for this marine ecosystem was obtained for the years 1998–2002 (Institute for Environment & Sustainability, EU Joint Research Center, Ispra, Italy). To obtain the P/B value, the 1998 data ($378.96 \, t \, km^{-2} \, year^{-1}$) was divided by the biomass estimate.

A.17. Discards

Trawlers discard 39% of the total catch (Machias et al., 2001), purse seiners 14% (Tsimenides et al., 1995), beach seiners 28% (Stergiou et al., 1996), netters and longliners 9.8% (Tzanatos et al., 2007). These percentages were used for the calculation of discard rates for the 1964 model. $0.1346 \, t \, km^{-2}$ was the calculated value.

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