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An indicator-based evaluation of Black Sea food web dynamics during 1960–2000

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ABSTRACT

Four Ecopath mass-balance models were implemented for evaluating the structure and function of the Black Sea ecosystem using several ecological indicators during four distinctive periods (1960s, 1980–1987, 1988–1994 and 1995–2000). The results exemplify how the Black Sea ecosystem structure started to change after the 1960s as a result of a series of trophic transformations, i.e., shifts in the energy flow pathways through the food web. These transformations were initiated by anthropogenic factors, such as eutrophication and overfishing, that led to the transfer of large quantities of energy to the trophic dead-end species, which had no natural predators in the ecosystem, i.e., jellyfish whose biomass increased from 0.03 g C m^{-2} in 1960–1969 to 0.933 g C m^{-2} in 1988–1994. Concurrently, an alternative short pathway for energy transfer was formed that converted significant amounts of system production back to detritus. This decreased the transfer efficiency of energy flow from the primary producers to the higher trophic levels from 9% in the 1960s to 3% between 1980 and 1987. We conclude that the anchovy stock collapse and successful establishment of the alien comb-jelly *Mnemiopsis* in 1989 were rooted in the trophic interactions in the food web, all of which were exacerbated because of the long-term establishment of a combination of anthropogenic stressors.

1. Introduction

The Black Sea ecosystem underwent significant trophic transformations over the second half of the 20th century (Oguz and Gilbert, 2007). The history of these changes can be classified into four distinct periods: 1) the 1960s — pre-eutrophication, 2) 1980–1987 — intense eutrophication years, 3) 1988–1994 — the *Mnemiopsis leidyi* (Agassiz, 1865) — anchovy shift, and 4) 1995–2000 — the post-eutrophication phase (Fig. 1). The principal reasons for these transformations have long been debated (Bilio and Niermann, 2004; Kideys et al., 2000; Kovalev and Piontkovski, 1998; Kovalev et al., 1998; McQuatters-Gollop et al., 2008; Oguz and Gilbert, 2007; Oguz et al., 2003; Shiganova, 1998; Yunev et al., 2002, 2007; Zaitsev, 1992). When primarily focusing on the anchovy — *Mnemiopsis* shift in 1989 (Kideys, 2002), studies sought answers to enhance the comprehension of the mechanisms underlying the observed changes (Berdnikov et al., 1999; Daskalov, 2002; Daskalov et al., 2007; Gucu, 2002; Llope et al., 2011; Oguz, 2007; Oguz et al., 2008a,b). The roles of the trophic cascade because of overfishing (Daskalov, 2002; Gucu, 2002), *M. leidyi* (hereafter called *Mnemiopsis*) predation on anchovy eggs and larvae (Kideys, 2002; Lebedeva and Shushkina, 1994; Shiganova and Bulgakova, 2000) and the combination of bottom-up and top-down controls (Bilio and Niermann, 2004; Oguz, 2007; Oguz et al., 2008a) were all suggested as significant processes catalysing the observed ecosystem changes.

The pre-eutrophication phase of the 1960s characterised a healthy mesotrophic ecosystem with primary production values between 100 and 200 mg C m^{-2} y^{-1} (Oguz et al., 2012). In the 1960s, relatively rich biological diversity of the Black Sea comprised fishes from large demersal fish species, such as turbot (*Psetta maeotica*; Pallas, 1814), Black Sea striped mullet (*Mullus barbatus ponticus*; Essipov, 1927), spiny dogfish (*Squalus acanthias*; Linnaeus, 1758), and Black Sea whiting (*Merlangius merlangus euxinus*; Nordmann, 1840), to piscivorous pelagic fish, such as Atlantic bonito (*Sarda sarda*; Bloch, 1973), bluefish (*Pomatomus saltator*; Linnaeus, 1776), and Atlantic mackerel (*Scomber scombrus*; Linnaeus, 1758), as well as small pelagic fish, predominantly the Black Sea anchovy (*Engraulis encrasicolus ponticus*; Alexandrov, 1927), Black Sea horse mackerel (*Trachurus mediterraneus ponticus*; Aleev, 1956), and Black Sea sprat (*Sprattus sprattus phalaericus*; Risso, 1827). Three cetacean species, the Black Sea common dolphin (*Delphinus delphis ponticus*; Barabash-Nikiforov, 1935), the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*; Barabasch, 1940), and the Black Sea harbour porpoise (*Phocoena phocoena relicta*; Abel, 1905) represented the top predators of the system. During the subsequent two decades, the stocks of both pelagic piscivorous fishes and marine mammals were overexploited and primary and secondary pelagic production increased

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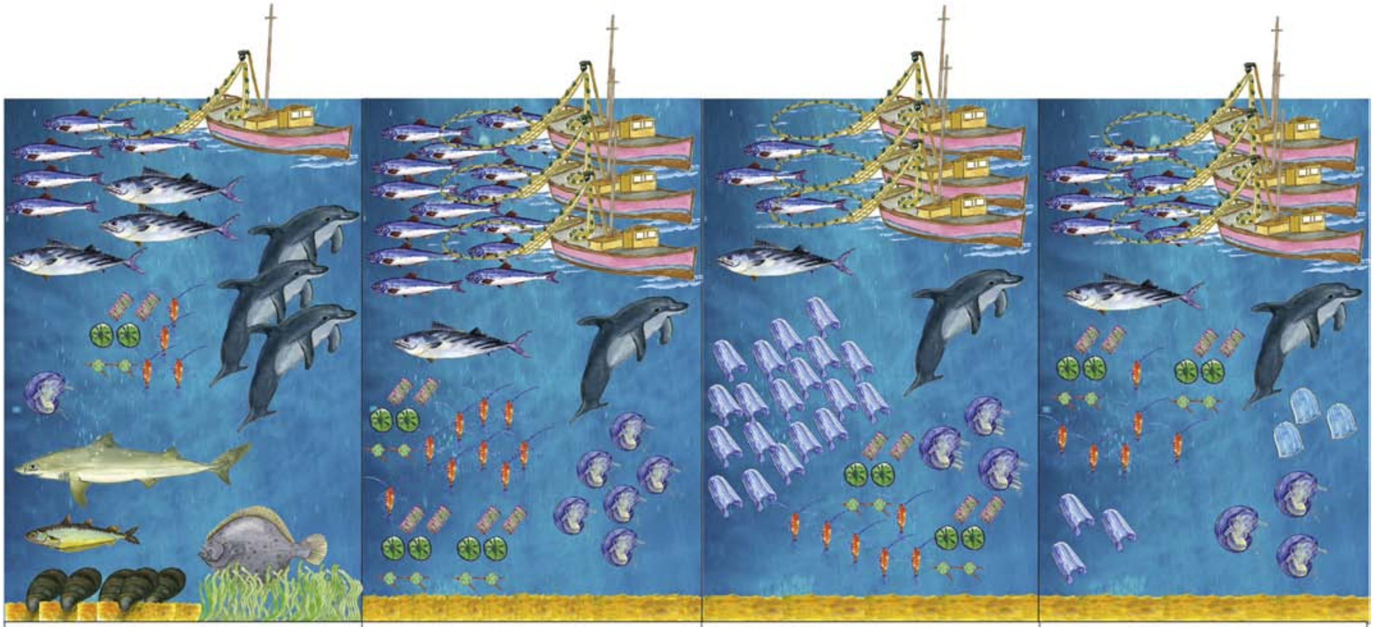

1950s and 1960s - Quasi-pristine	1970s and 1980s - Eutrophication	1989 - 1994 - Depression	1995 - 2000 - Aftermath
• Low nutrients. • Primary and secondary production is comparable to the Mediterranean Sea. • Diverse fish fauna. • Rich benthic life. • Modest fishing fleet. Catch ~ 200 kt.	• Excess nutrient input via rivers. • High primary and secondary production. • Pronounced quantities of jellyfish *Aurelia aurita*. • Fish fauna dominated by small pelagic fish. • Huge fishing fleet. Catch ~ 500 kt.	• Moderate nutrient levels. • Moderate primary and secondary production. • Outburst of alien ctenophore *Mnemiopsis leidyi*. • Fish stocks and fisheries collapsed. Catch ~ 150 kt.	• Moderate nutrient levels. • Moderate primary and secondary production. • Retreating biomass of *Mnemiopsis leidyi*. • Introduction of *Beroe ovata*, which predates only on *Mnemiopsis leidyi*. • Small pelagic fish stocks recovered to moderate levels. Catch ~ 300 kt.

Fig. 1. The schematic illustration of the four periods in the Black Sea. The figure was depicted based on the classifications in the published literature and derived from an earlier work (Fig. 10) in Langmead et al. (2007).

excessively because of nutrient enrichment from rivers discharging mainly into the northwestern shelf of the Black Sea. The small pelagic fish species and the moon jelly, *Aurelia aurita* (Linnaeus, 1758), became dominant in the ecosystem. The benthic flora and fauna greatly deteriorated because of the frequent hypoxia events of the shelf waters (Mee, 2006; Zaitsev, 1992; Zaitsev and Mamaev, 1997). Simultaneously, the Turkish fishing fleet grew enormously in size and technology (Gucu, 2002), and the fishery yield attained 700 kt, a significant proportion (~500 kt) of which consisted of anchovy. In 1989, the non-indigenous comb jelly species *Mnemiopsis*, which was introduced to the Black Sea ecosystem in the early 1980s via the ballast waters of shipping vessels, flourished in both abundance and biomass. This same year also coincided with the collapse of the Turkish fishery yield from an average of 700 kt during the early 1980s to only 150 kt in 1989 (Oguz, 2007). Subsequently, the Turkish fishery yield recovered to approximately 300 ± 100 kt, whereas it remained at very low levels throughout the rest of the Black Sea (Oguz et al., 2012). During this recuperation period, blooms of *Mnemiopsis* were suppressed naturally because of the appearance of another non-indigenous gelatinous species, *Beroe ovata* (Mayer, 1912), a natural *Mnemiopsis* predator. By the end of the 1990s, the entire Black Sea ecosystem was characterised by moderate primary (200–400 mg C m^{-2} y^{-1}, Oguz et al., 2012) and secondary productivity (McQuatters-Gollop et al., 2008; Mee, 2006), although the ecosystem of the northwestern shelf and western coastal waters was still far from recovery and rehabilitation (Oguz and Velikova, 2010).

To investigate the changes summarised above and their underlying causes, the various aspects of the Black Sea lower trophic food web function were studied in terms of aggregated biogeochemical models (e.g., Grégoire and Friedrich, 2004; Gregoire and Lacroix, 2003; Gregoire and Soetaert, 2010; Gregoire et al., 2004, 2008; He et al., 2012; Lancelot et al., 2002; Oguz and Merico, 2006; Oguz et al., 2000, 2001, 2008b; Staneva et al., 2010; Tsiaras et al., 2008). Additionally, mass-balance models of different complexities were also set-up by Gucu (2002), Daskalov (2002), and Orek (2000). Gucu (2002) focused on the second half of the 1980s when examining the role of increased fishing pressure on the collapse of anchovy stocks, whereas Daskalov (2002) adopted a broader time frame, starting from the pre-eutrophication period, and noted that trophic cascades that were initiated by overfishing played a leading role in ecosystem changes. However, both of these studies lacked the quantification of ecosystem characteristics of the Black Sea during these changes. Here, we expand upon these previous studies by i) using a set of indicators that quantify the condition of the ecosystem to systematically analyse each defined ecosystem period and, ii) providing an understanding of the interactions between the food web components that led to the aforementioned changes in the Black Sea. The ecological analyses were performed within the framework of "ecosystem health", which will ultimately provide reference points to evaluate the transformations of the Black Sea's ecosystem structure and function over recent decades based on quantitative ecosystem metrics. Here, ecosystem health was used to define the potential of an ecosystem under stress to sustain its structure and function over time (Costanza, 1992; Costanza and Mageau, 1999; Haskell et al., 1992; Schaeffer et al., 1988). The methodology that was adopted to assess ecosystem health comprised the application of ecological network analysis (Ulanowicz, 1986) on the mass-balance models of the ecosystem and in the utilisation of derived ecological indicators to characterise the distinctive prevailing conditions of the four ecosystem periods that are described above. The indicators were used to assess the "ecological health" of the Black Sea ecosystem in the four periods and to investigate the reasons behind the prevailing conditions observed in them. This study may be considered the first to employ ecological indicators to analyse and evaluate historical food web changes in this particularly exploited and biologically diverse ecosystem.

2. Materials and methods

The static mass-balance modelling of the food web was implemented by developing an Ecopath (Christensen et al., 2005) food web model for each period. The Ecopath models of the Black Sea were built to represent the general food web structure of the inner Black Sea basin, avoiding the extremely variable conditions of the northwestern shelf (NWS). The model covers an area of 150,000 km^2 where fisheries operate intensively (Oguz et al., 2008a) in the vicinity of the exclusive economic zones (EEZs) of the six riparian countries (Fig. 2). The geographical representation of the model does not include depths greater than 150 m in the open Black Sea where anoxia prevails.

2.1. The model set-up

Four mass-balance Ecopath models were set-up to represent the four distinctive periods of the Black Sea ecosystem that were described in the Introduction. An Ecopath model comprises a set of functional groups (each representing a species or groups of species) that are linked by trophic interactions. The functional groups are regulated by gains (consumption, immigration) and losses (mortality, emigration) and are linked to one another by predator–prey relationships. Fisheries extract biomass from the targeted and by-catch groups. A linear equation describes flows of mass, energy or nutrients into and out of each functional group i:

$$B_i * \left(\frac{P}{B}\right)_i - \sum_{j=1}^{n} B_j * \left(\frac{Q}{B}\right)_j * DC_{ji} - B_i * \left(\frac{P}{B}\right)_i * (1-EE_i) - Y_i - E_i - BA_i = 0 \quad (1)$$

in which B indicates biomass, $(P/B)_i$ indicates the production to biomass ratio, $(Q/B)_j$ indicates the consumption to biomass ratio of predator j, DC_{ji} is the fraction of prey i in the average diet of predator j, Y is the landings, E is the net migration rate, BA is the biomass accumulation rate, and EE (ecotrophic efficiency) is the proportion of the production utilised in the system (Christensen et al., 2005). EE must be less than or equal to unity under the assumption of mass-balance. E and BA values were assumed to be zero for all groups. Typically, three of B, (P/B), (Q/B) or (P/Q) and EE parameters and diet composition are defined as input for each functional group, and the values of remaining parameters are estimated by the Ecopath mass-balance algorithm. Ecopath software computes mass-balance by solving the system of equations for the unknown parameters of all groups. A balanced model, however, might not be obtained at the first parameterisation, thus it may require iterative adjustments to the input values (usually the diet composition) following the guidelines given by Christensen et al. (2005).

The model set-up in this investigation presented a simplified representation of the pelagic food web structure using ten functional groups (Table 1), six of which were the guilds of ecologically similar species, namely dolphins, pelagic piscivorous fish, demersal fish, small pelagic fish, zooplankton and phytoplankton, whereas the other three groups represented individual species; the comb jelly *Mnemiopsis*, the moon jelly *A. aurita* (hereafter called as *Aurelia*) and the heterotrophic dinoflagellate *Noctiluca scintillans* (Ehrenberg, 1834) (hereafter called as *Noctiluca*). These organisms were represented separately because they played specific roles (r-selected behaviour; Pianka, 1970) in ecosystem functioning and were important indicators of ecosystem changes during the specified periods. Because the aim of the present study was to

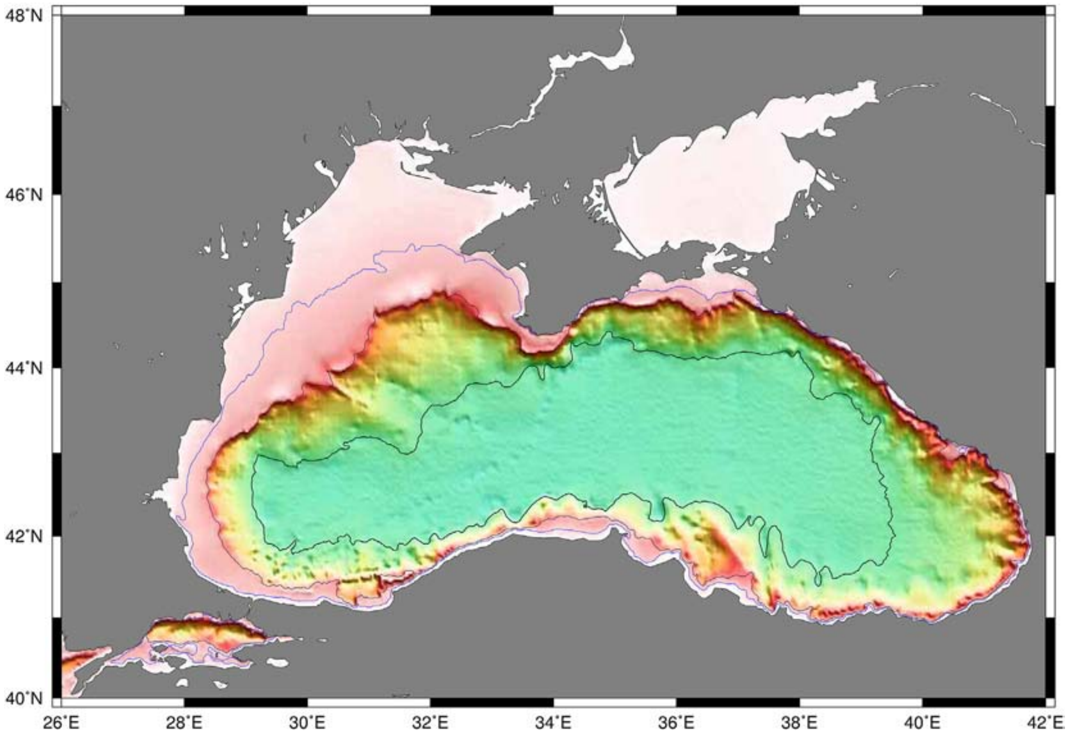

Fig. 2. The model domain (the region constrained between the coastline and the 2000 m contour) in the Black Sea. The contours are for isobaths of 50 m (blue curve), 200 m (thin black curve) and 2000 m (thick black curve).
From Liu and Dittert (2010).

Table 1
Trophic groups and main species included in the model set-up.

Groups	Main species
Dolphins	Black Sea common dolphin
	Black Sea bottlenose dolphin
	Black Sea harbour porpoise
Pelagic piscivorous fish	Bluefish
	Atlantic bonito
	Atlantic mackerel
Demersal fish	Black Sea whiting
	Black Sea turbot
	Black Sea striped mullet
Small pelagic fish	Black Sea anchovy
	Black Sea sprat
	Black Sea horse mackerel
Aurelia	*Aurelia aurita*
Mnemiopsis	*Mnemiopsis leidyi*
Noctiluca	*Noctiluca scintillans*
Zooplankton	Mesozooplankton
	Microzooplankton
Phytoplankton	Diatoms
	Dinoflagellates
Detritus	POM + detritus

investigate the changes in ecosystem structure of the Black Sea and not the interactions among different types of fisheries, fisheries were collectively represented, although the Black Sea industrial fisheries included mainly three methods: trawling, gill-netting and seining. Thus, a single fleet was considered in the model, and fishery yields by species were pooled to ensure correctly aggregated catches for each functional group. For each modelled state of the Black Sea, an average annual catch value was calculated from the data for the period investigated. The average value was then divided by the total area of the fishing grounds (150,000 km^2; Oguz et al., 2008a) to obtain the yield per unit fishing area.

Each ecosystem period was described by key parameters and input data for each functional group, such as biomass per unit area, rates of production and consumption, diet composition, and fishery losses. The units were in g C m^{-2} y^{-1} for quantities and y^{-1} for rates. Models that include jellyfish should be built considering that a significant portion of the wet weight of these organisms is water. Hence, because our model set-up included gelatinous organisms as important components of the food web, carbon weight was used as the model currency, as suggested by Pauly et al. (2009). Considering that the catch statistics and in-situ data that are available in the literature were in tonnes and grammes wet weight per square metre, respectively, the values were converted into grammes carbon per square metre using conversion factors specific to the concerned group; these are listed in Table 2.

Because of data availability, the biomass values for dolphins and pelagic piscivorous fish were used as input parameters for the 1960s model set-up, and the *EE* values estimated by the Ecopath model for these two functional groups were used as input for the remaining three model set-ups because of the lack of biomass estimates for these organisms in the respective modelled periods. The *EE* parameters for all of the remaining groups were calculated by the model in all model set-ups. The fraction of the consumption that is not assimilated was set to the Ecopath's default value of 0.2 for all groups. The fishery yields along with other input values used to parameterise the four Ecopath models are summarised in Table 3. The input data were derived from the literature and previously published mass-balance modelling studies concerning the Black Sea and used with slight rounding modifications. However, the input *P*/*B* and *Q*/*B* parameters for *Mnemiopsis* were not taken from the literature, but were assumed to be identical to *Aurelia*'s. Furthermore, because the input parameters that were inherited from previously published models comprised more functional groups (e.g., microzooplankton and mesozooplankton in Daskalov (2002)) compared to the model set-up used in this study (e.g., zooplankton), the weighted average values of the input parameters for such groups were computed and used in the four mass-balance models.

Table 2
Multipliers used to convert biomass and catch values from grammes wet weight into grammes carbon.

Group	Conversion multiplier (grammes wet weight to grammes carbon)	Reference
Phytoplankton	0.1	O'Reilly and Dow (2006)
Zooplankton	0.08	Dow et al. (2006), Weslawski and Legeżyńska (1998)
Noctiluca	0.08	Dow et al. (2006)
Aurelia	0.002	Oguz et al. (2001)
Mnemiopsis	0.001	Oguz et al. (2001)
Fish groups	0.11	Oguz et al. (2008a)

The diet composition matrix that incorporated the relative proportions of predation on each group followed those from previous studies by Gucu (2002) and Daskalov (2002) except for some specific adjustments (Table 4). The diets of small pelagic fish and demersal fish were taken from Gucu (2002) and used without modifications. The model of Gucu (2002) only included one jellyfish group by pooling all of the jellyfish species (*Aurelia*, *Mnemiopsis* and *Pleurobrachia pileus*) in the Black Sea. Because the model set-up used in our study included distinctive groups for *Aurelia* and *Mnemiopsis* and completely excluded *Pleurobrachia*, their diets were assumed to be identical, and therefore, the diet composition given in Gucu (2002) for the jellyfish group was used for these two groups. The diet of the zooplankton group was taken from Gucu (2002) (50% phytoplankton and 50% detritus); however, modified to include 60% phytoplankton and 40% detritus, assuming that zooplankton preferentially graze on phytoplankton rather than detritus. The diet of piscivorous fish was also taken from Gucu (2002) (50% small pelagic fish, 10% demersal fish and 40% import) but modified to include 60% small pelagic fish and 40% import by excluding the demersal fish group in their diet. The omission of demersal fish was made considering that the habitat distributions of these two groups are quite distinct, and therefore, the piscivorous fish group was inclined to consume more of the small pelagic fish group. The diet of dolphins was taken from Daskalov (2002) (96% small pelagic fish, 3.5% demersal fish and 0.5% piscivorous fish), however, it was modified to include 90% small pelagic fish, 9.5% demersal fish and 0.5% piscivorous fish to obtain mass-balance. The diet items of *Noctiluca* were constructed following Oguz et al. (2001), who included its grazing on phytoplankton, zooplankton and detritus. The relative proportions of the items in the diet of *Noctiluca* were determined following Umani et al. (2004).

2.2. Ecological indicators

The four ecosystem periods were examined by utilising several indicators that were provided by the Ecopath model package using the final mass-balance biomass and flow estimates. Mixed trophic impact (MTI) analysis was performed to analyse the relative direct and indirect effects of variation within a group's biomass on the biomass of the other groups (Ulanowicz and Puccia, 1990). The direct impact of any one group upon another, related to predation or fishing, might cascade to other groups by any order of indirect interaction. MTI enables the quantification of all possible direct and indirect interactions between two groups. By defining MTI ([*M*]) as the product of all of the impacts that group *i* has on group *j*, it is calculated as

$$[M] = \{[I]-[Q]\}^{-1}-[I] \tag{2}$$

in which *Q* denotes the net impact matrix comprising impacts between all the groups in the food web, and I signifies the identity matrix (Ulanowicz and Puccia, 1990). The elements *qij* of matrix *Q*, are obtained by the difference *dji* - *fij*, where d_{ji} denotes the positive effects that *i* has on *j* and is calculated by the means of the fraction of prey *i* in the

Table 3
Input parameters of functional groups in four model periods. Catch values were obtained from Prodanov et al. (1997) and complemented from Shlyakhov and Daskalov (2008). *P*/*B* and *Q*/*B* values are from Daskalov (2002). Biomass estimations of groups in 1960–1969 were from Daskalov (2002). Biomass estimates for the later periods for fish groups were from Shlyakhov and Daskalov (2008) and for lower-trophic-level groups were from Shiganova et al. (2008), except the phytoplankton group, in which biomass values were from Nesterova et al. (2008). Estimated *EE* values of dolphins and pelagic piscivorous fish in 1960–1969 were used in the models of the later periods as inputs. “Est.” stands for “estimated” and denotes parameters that were computed by the Ecopath mass-balance algorithm. P1, P2, P3 and P4 denote model periods 1960–1969, 1980–1987, 1988–1994 and 1995–2000, respectively. "N.A." stands for "not applicable".

Groups	Biomass ($g\,C\,m^{-2}$)				Production/Biomass (y^{-1})				Consumption/Biomass (y^{-1})				Ecotrophic efficiency				Catch ($g\,C\,m^{-2}\,y^{-1}$)			
	P1	P2	P3	P4	P 1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Dolphins	0.010	Est.			0.350				19.000				Est.	0.286			0.001			
Pelagic piscivorous fish	0.020	Est.			0.550				5.000				Est.	0.995			0.010	0.026	0.016	0.006
Demersal fish	0.050	0.329	0.121	0.086	0.630				1.500				Est.				–	0.021	0.024	0.016
Small pelagic fish	0.200	1.457	0.538	0.553	1.500				11.000				Est.				0.020	0.410	0.170	0.245
Aurelia	0.030	0.480	0.112	0.128	11.000				29.200				Est.				N.A.			
Mnemiopsis	–	–	0.821	0.176	–	–	11.000		–	–	29.200		Est.				N.A.			
Zooplankton	0.660	0.903	0.540	1.207	44.000				345.000				Est.				N.A.			
Noctiluca	0.090	1.060	0.736	0.500	7.300				36.200				Est.				N.A.			
Phytoplankton	0.880	1.950	1.950	1.194	291.000				N.A.				Est.				N.A.			

diet of the predator j, and f_{ij} signifies the negative effects that j has on i, calculated using the fraction of the total consumption of prey i that is used by predator j (Libralato et al., 2006). Mixed trophic impact values scale between −1 (strong negative impact) and 1 (strong positive impact) and are relative measures of the interactions between two groups. Negative values indicate an inhibiting effect and positive values indicate a promoting effect between two corresponding groups.

Furthermore, keystone functional groups were determined for each model period. Keystone groups are groups or species with relatively low biomass values despite having an important functional role in their ecosystems (Power et al., 1996). The keystone value of each group is calculated as

$$KS_i = \log[\varepsilon_i(1-p_i)] \tag{3}$$

in which KS_i is the keystoneness of group i, and p_i is the ratio of the biomass of group i (B_i) to the sum of the biomass values of all groups and is calculated as

$$p_i = \frac{B_i}{\sum B_i} \tag{4}$$

following Libralato et al. (2006).

The transfer efficiency (TE) is an index to measure the efficiency with which energy is transferred between adjacent trophic levels. It is calculated as the ratio of aggregated production of a trophic level to the aggregated production of the preceding trophic level (Lalli and Parsons, 1993). Thus, the primary producers and detritus groups are conventionally attributed to TL I, the herbivorous fraction of flows and biomasses to TL II, the first order carnivorous flows and biomasses to TL III and the second order carnivorous flows and biomasses are attributed to TL IV. This classification allowed us to distinguish biomasses and flows along the primary producer-based and the detritus-based food-chains. Here, transfer efficiencies were calculated by disaggregating functional groups' biomasses and flows at each integer trophic level (TL), and then aggregating the results by integer TLs as defined by Lindeman (1942).

Additionally, some commonly used ecosystem indices and synthetic ecological indicators were also employed in assessing the ecological status of the Black Sea ecosystem for the four model periods (Table 5). These indicators were chosen because they could easily be calculated by using simple mathematical algorithms. They can be derived with the utilisation of basic network theory and are readily integrated into several ecological network and mass-balance analysis packages such as Ecopath.

3. Results

3.1. Model outputs

The mass-balance models calculated the ecotrophic efficiency values of all groups in the first period (Table 6). In the latter periods, because of the lack of stock assessment studies for dolphins and pelagic piscivorous fish, the ecotrophic efficiency values calculated in the first period were used for these two groups as input parameters, and their biomass values were computed by the mass-balance algorithm (Table 6). For all other functional groups, ecotrophic efficiency values were calculated by the model for periods two, three and four. Furthermore, respiratory flows for all functional groups were calculated from the energetic balance of the sources and sinks in each functional compartment (Table 6) as the model product and were in compliance with the energy budget of each state variable that was described in the model, which assumed

Table 4
Diet composition matrix used in all model periods (compiled mainly from Gucu (2002) and Daskalov (2002)). The details are explained in the text.

Group/species	Dolphins	Pelagic piscivorous fish	Demersal fish	Small pelagic fish	*Aurelia*	*Mnemiopsis*	Zooplankton	*Noctiluca*
Dolphins								
Pelagic piscivorous fish	0.05							
Demersal fish	0.095		0.1					
Small pelagic fish	0.9	0.60	0.35					
Aurelia								
Mnemiopsis								
Zooplankton			0.2	1.00	0.5	0.5		0.15
Noctiluca								
Phytoplankton					0.10	0.10	0.60	0.60
Detritus			0.35		0.40	0.40	0.40	0.25
Import		0.4						

Table 5
Ecosystem indices and synthetic ecological indicators used to assess the ecological status of the Black Sea ecosystem in the four model periods.

Indicator	Explanation	Units
Total System Throughput (TST)	The sum of all flows within the ecosystem (Odum, 1971).	$g\,C\,m^{-2}\,y^{-1}$
Total primary production/Total Respiration (TPP/TR)	Ratio of total primary production in the system to the sum of all respiratory flows (Odum, 1971). In mature ecosystems, this ratio is close to unity (Tomczak et al., 2009).	–
Net system production	This equals primary production minus respiratory flows in the system. In mature ecosystems, this difference is expected to be near zero (Christensen, 1995).	$g\,C\,m^{-2}\,y^{-1}$
Total primary production/total biomass	This ratio is expected to be low in mature ecosystems and high in developmental stages (Christensen, 1995).	–
Mean trophic level of the catch (mTL_c)	As fishing pressure increases, the mean trophic level of the catch is expected to decrease (Pauly et al., 1998).	–
System Omnivory Index (SOI)	Average omnivory index (food spectrum) of all consumers weighted by each consumer's consumption (Christensen et al., 2005). The higher the SOI, the more web-like the ecosystem's food chain.	–
Finn's Cycling Index (FCI)	A measure of TST recycled in the ecosystem. This value is expected to be high in mature ecosystems (Finn, 1976).	–
Finn's mean path length	The average number of steps along which the system production flows through the ecosystem. In mature ecosystems this value is expected to be high (Finn, 1976).	–
Primary production required (PPR)	This is the amount of primary production required to sustain the given amount of catches within the ecosystem (Odum, 1971).	$g\,C\,m^{-2}\,y^{-1}$
Ratio of predatory fish biomass to forage fish biomass	This ratio is an indicator of the "fishing down the food web" effect as a result of harvesting top predatory fish species. It is expected to decrease with fishing (Shannon et al., 2009).	–
Ratio of jellyfish biomass to the sum of all zooplankton biomass	This ratio indicates the importance/dominance of jellyfish in the entire zooplankton community. It is expected to increase with fishing (Shannon et al., 2009).	–
Ratio of demersal fish to pelagic fish	This ratio is an indicator of the "fishing down the food web" effect as a result of harvesting top predatory fish species. It is expected to decrease with fishing (Shannon et al., 2009).	–

that the consumption of a group was the sum of production, respiration, and unassimilated food. The increases in respiratory flows of zooplankton and gelatinous organisms as well as small pelagic fish from the first period to the second and third periods were remarkable. From system development theory (Odum, 1969), the increase in respiratory flows is a sign of perturbed food web conditions. The decrease in the estimated biomass values of piscivorous fish from the first period to the latter periods was also pronounced and found to correspond with explanations provided by other studies (Gucu, 2002; Oguz, 2007).

The primary production values that were calculated by the model were 256, 567, 567 and 347.5 mg C m^{-2} d^{-1} for the four periods, respectively. The primary production values were found to be marginally overestimated for the first period (100–200 mg C m^{-2} d^{-1}) and underestimated for the second and third periods (600–800 mg C m^{-2} d^{-1} for 1975–1990), and in the last period, primary production matched the literature averages (200–400 mg C m^{-2} d^{-1}) (Oguz et al., 2012; Yunev et al., 2002 from in-situ data and model estimations).

3.2. Mixed trophic impact

The MTI analysis was performed to reveal the impacts of fisheries on the exploited species, interspecies competition among gelatinous organisms and small pelagic fish, and the predation impact of the opportunistic species *Noctiluca* on zooplankton and phytoplankton groups (Fig. 3). According to the results, fisheries had positive mixed trophic impacts on demersal (0.489) and small pelagic fish (0.308) groups, whereas it caused negative impacts on dolphin (−0.650) and pelagic piscivorous fish (−0.645) groups for the period 1960–1969. The positive impacts of fisheries on small pelagic and demersal fish groups resulted from the fact that the direct negative impacts because of harvesting were exceeded by the positive indirect impacts, i.e., the exploitation of their predators; dolphins and pelagic piscivorous fish. Conversely, in the model period 1980–1987, the fishery impacts on all fish groups and dolphins were negative (−0.954 for dolphins, −0.865 for piscivorous fish, −0.029 for demersal fish and −0.058 for small pelagic fish) because of the increasing exploitation rates exerted by fisheries on all target groups. The fishery impact on small pelagic fish groups became positive (0.120) during 1988–1994 because of the collapse of the small pelagic fishery and its respective stocks, generating a shift in the fishery, hence, realising the relatively more intensive targeting of demersal and pelagic piscivorous fish groups. The fishery impacts were calculated as negative for small pelagic fish (−0.055) and positive for demersal fish (0.036) during 1995–2000 because of the recovery of the small pelagic fishery, allowing some release of fishing pressure on the demersal fish species along with more intensive targeting of small pelagic fish. As expected, the fishery exerted negative impacts on all other targeted groups in the four periods.

Because the gelatinous species *Aurelia* had a preference for zooplankton consumption, its MTI on the small pelagic fish group was negative (−0.0477 for 1960–1969 and −0.0856 for 1980–1987). After the explosion of *Mnemiopsis*, *Aurelia*'s impact remained negative, but the MTI values diminished by nearly half to −0.0285 and −0.0473 during 1988–1994 and 1995–2000, respectively. On the contrary, *Mnemiopsis* maintained a stronger negative impact on the small pelagic fish groups (−0.209 and −0.0650) during the latter two periods.

Direct predation of the heterotrophic dinoflagellate *Noctiluca* exerted a negative mixed trophic impact on the zooplankton group (−0.0673 in 1960–1969, −0.122 in 1980–1987, −0.116 in 1988–1994 and −0.107 in 1995–2000) in all periods. A notable significant change occurred between the first and the second time periods because of increasing *Noctiluca* biomass corresponding with the degradation of the food web. However, *Noctiluca*'s mixed trophic impact on the phytoplankton group was positive (0.0517) in 1960–1969 because *Noctiluca*'s direct negative impact on phytoplankton (predation) was outcompeted by its indirect positive effect, which was the consumption of the main predator of phytoplankton, i.e., zooplankton. In the model period 1988–1994, the impact of *Noctiluca* on phytoplankton was negative (−0.0197) because of *Noctiluca*'s increasing biomass concentration in the ecosystem. For the last period (1995–2000), the impact of *Noctiluca* on phytoplankton was positive (0.059) because of its diminishing

Table 6
Basic output parameters calculated by the Ecopath for the four modelled periods. P1, P2, P3 and P4 denote model periods of 1960–1969, 1980–1987, 1988–1994 and 1995–2000, respectively.

Parameter/group	Ecotrophic efficiency				Biomass (g C m^{-2} y^{-1})				Respiration (g C m^{-2})			
	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Dolphins	0.296				–	0.01	0.01	0.01	0.15	0.15	0.15	0.15
Piscivorous fish	0.995				–	0.05	0.03	0.01	0.07	0.17	0.11	0.05
Demersal fish	0.811	0.427	0.791	0.862					0.03	0.19	0.07	0.05
Small pelagic fish	0.924	0.413	0.618	0.603					1.46	10.64	3.93	4.04
Aurelia	0								0.37	5.93	1.38	1.58
Mnemiopsis	0								–	–	10.15	2.18
Zooplankton	0.108	0.727	0.992	0.25					153.1	209.50	125.30	280.0
Noctiluca	0								1.949	22.96	15.94	10.83
Phytoplankton	0.541	0.372	0.230	0.753					–			
Detritus	0.483	0.306	0.183	0.783					–			

biomass values. In the model period of 1980–1987, *Noctiluca* had a slightly negative impact on the phytoplankton group.

3.3. Keystoneness

The keystoneness index (KS) of the functional groups showed relevant differences in the four time periods (Fig. 4). In all periods, with the exception of 1960–1969, the zooplankton group had the highest KS values. In 1960–1969, the dolphin group acquired the highest KS value of −0.143, and this was followed by comparable KS values of zooplankton (−0.404), small pelagic fish (−0.428), phytoplankton (−0.532) and piscivorous fish (−0.561), suggesting the dolphins' top-down control on the lower trophic levels. The first period displayed much smaller KS values (around −1) for the heterotrophic dinoflagellate *Noctiluca* and jellyfish *Aurelia*, along with the demersal fish group because of their marginal dominance during the first period. However, the keystoneness indices of *Aurelia* and *Noctiluca* increased slightly to −0.772 and −0.881, respectively, closely following the KS value of small pelagic fish (−0.623) in 1980–1987. This contrasted with a major reduction in the dolphins' keystone level to −0.75 and similar reductions in the KS values of the piscivorous and demersal fish groups (−0.913, −1.028, respectively). This decline suggested a decrease in the top-down predatory control mechanism on the intermediate trophic level species. In the third period, 1988–1994, *Mnemiopsis* was the secondary keystone species of significance after zooplankton, with a KS index value of −0.46. It was followed by the dolphin and phytoplankton groups with index values of −0.491 and −0.498, respectively. The KS values of small pelagic fish, pelagic piscivorous fish, *Noctiluca*, and *Aurelia* were

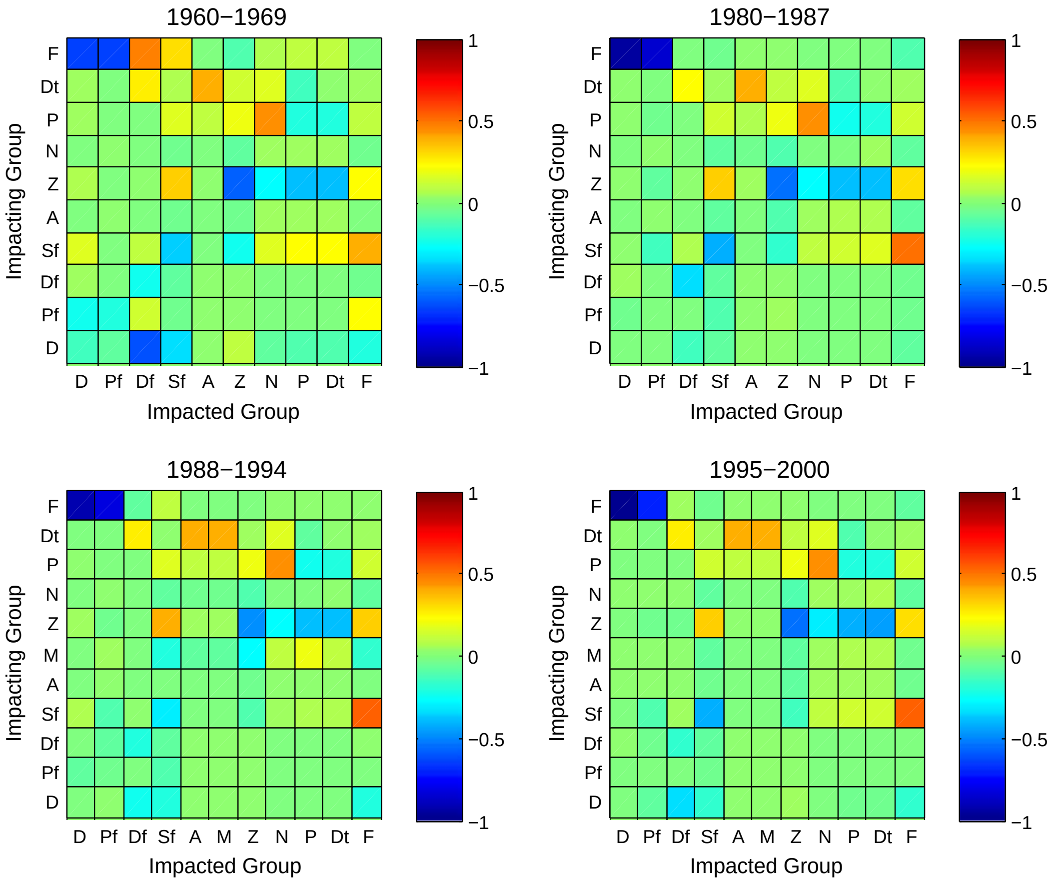

Fig. 3. Mixed trophic impact relationships between functional groups in the four model periods. Abbreviations: F (fisheries), Dt (detritus), P (phytoplankton), N (*Noctiluca*), Z (zooplankton), M (*Mnemiopsis*), A (*Aurelia*), Sf (small pelagic fish), Df (demersal fish), Pf (pelagic piscivorous fish), D (dolphins).

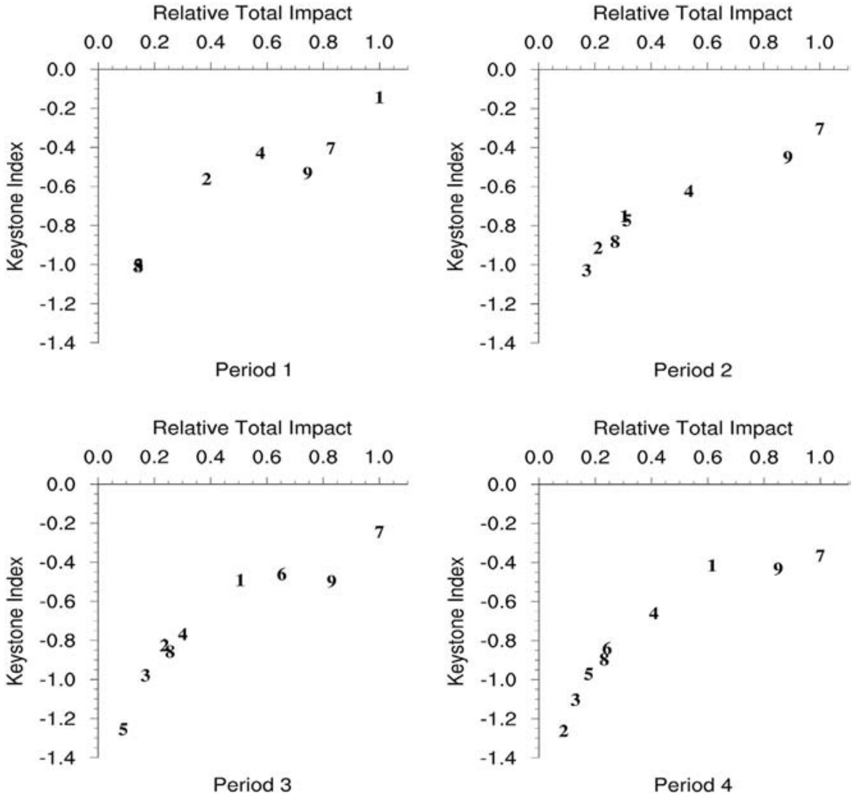

Fig. 4. Keystoneness and relative total impact of functional groups on the structure of the Black Sea food web in four model periods. 1) Dolphins, 2) piscivorous fish, 3) demersal fish, 4) small pelagic fish, 5) *Aurelia*, 6) *Mnemiopsis*, 7) zooplankton, 8) *Noctiluca*, 9) phytoplankton.

calculated as −0.767, −0.824, −0.857 and −1.255, respectively. During the last period, 1995–2000, dolphin, phytoplankton, and small pelagic fish groups followed the zooplankton group in terms of keystoneness, with KS values of −0.414, −0.433 and −0.659, respectively. The keystoneness of *Mnemiopsis* decreased to −0.839 following the small pelagic fish. *Noctiluca* followed *Mnemiopsis* with a keystone index value of −0.896. *Aurelia*, demersal fish, and piscivorous fish groups were the last three groups with KS index values of −0.971, −1.203 and −1.262, respectively.

3.4. Trophic flow and transfer efficiency

The overall transfer efficiency from the producer and detritus compartments (TL I) to TL II increased from 1.4% in 1960–1969 to 8.2% in 1980–1987 and 10.6% in 1988–1994, indicating strengthened bottom-up effects in the food web during those periods, but decreased to 3% in the last time period (Table 7). However, the transfer efficiency from TL II to TL III decreased from 8.9% in 1960–1969 to 3.2% in 1980–1987 and 2.2% in 1988–1994 because TL III comprised both the small pelagic fish and a given portion of flows attributed to jellies, in which the latter constituted a larger share of the biomass during these periods. Finally, as jelly biomasses declined to moderate values, the transfer efficiency from TL II to TL III increased slightly to 3.8% in 1995–2000. The transfer efficiencies of all flows from TL III to TL IV were calculated as 6.3%, 7.3%, 8.7% and 7.4% in the four modelled periods, respectively. Considering the transfer efficiency from TL IV to TL V, a rough estimate of 0.5% was calculated for each period; however, this estimate was biassed by the relatively low dolphin biomass because of the lack of reliable observational data.

3.5. Summary statistics and synthetic indicators

The results of the analyses of the synthetic indicators and the statistical parameters (Table 8) calculated for the four model periods are summarised in this section. Total System Throughput (TST) increased from 681.733 g C m^{-2} y^{-1} in the period 1960–1969 up to 1405.977 g C m^{-2} y^{-1} in 1980–1987 with increasing productive capacity of the ecosystem because of eutrophication. In the periods 1988–1994 and 1995–2000, TST values were calculated as 1316.583 g C m^{-2} y^{-1} and 1020.347 g C m^{-2} y^{-1}, respectively.

Net system production increased from 98.934 g C m^{-2} y^{-1} in 1960–1969 to 317.918 g C m^{-2} y^{-1} in 1980–1987. In 1988–1994 and 1995–2000, net system production was calculated as 410.443 g C m^{-2} y^{-1} and 48.563 g C m^{-2} y^{-1}, respectively. The ratio of total primary production to the sum of all respiratory flows in the system was calculated as 1.63 in 1960–1969. In 1980–1987, this ratio increased to 2.274. It further increased to 3.614 in 1988–1994. In 1995–2000, this ratio decreased to 1.162.

Table 7
Transfer efficiency (%) of flows across trophic levels in the four modelled periods.

Source/trophic level	1960–1969				1980–1987				1988–1994				1995–2000			
	II	III	IV	V	II	III	IV	V	II	III	IV	V	II	III	IV	V
Producer	1.4	9.0	6.3	0.5	8.2	3.2	7.3	0.5	10.8	2.2	8.7	0.5	3.0	3.8	7.4	0.5
Detritus	1.4	8.9	6.3	0.5	8.3	3.2	7.3	0.5	10.3	2.2	8.7	0.5	3.0	3.8	7.4	0.5
All flows	1.4	8.9	6.3	0.5	8.2	3.2	7.3	0.5	10.6	2.2	8.7	0.5	3.0	3.8	7.4	0.5

Table 8
Summary statistics and flow indices of the four mass-balance models of the Black Sea ecosystem for their respective periods.

Parameter/period	1960–1969	1980–1987	1988–1994	1995–2000	Units
Summary statistics					
Sum of all consumption	234.399	380.882	246.634	449.859	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Sum of all exports	98.974	318.017	410.506	48.589	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Sum of all respiratory flows	157.146	249.532	157.007	298.891	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Sum of all flows into detritus	191.214	457.545	502.436	223.008	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Total System Throughput	681.733	1405.977	1316.583	1020.347	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Sum of all production	286.453	622.624	607.750	408.450	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Mean trophic level of the catch	3.355	3.065	3.095	3.033	–
Gross efficiency (catch/net p.p.)	0.000	0.001	0.000	0.001	–
Calculated total net primary production	256.080	567.450	567.450	347.454	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Total primary production/Total Respiration	1.630	2.274	3.614	1.162	–
Net system production	98.934	317.918	410.443	48.563	$\mathrm{g\,C\,m^{-2}\,y^{-1}}$
Total primary production/total biomass	132.000	90.955	116.771	89.847	–
Total biomass/total throughput	0.003	0.004	0.004	0.004	$\mathrm{y^{-1}}$
Total biomass (excluding detritus)	1.940	6.239	4.860	3.867	$\mathrm{g\,C\,m^{-2}}$
Primary production required/Total PP (PPR/TotPP)	6.873	52.815	25.836	28.930	%
Network flow indices					
System Omnivory Index	0.072	0.122	0.115	0.116	–
Finn's Cycling Index	9.400	4.610	2.760	15.010	(% of TST)
Finn's mean path length	2.662	2.477	2.320	2.936	–

The mean trophic level of the catch ($\mathrm{mTL_c}$) decreased from 3.36 in 1960–1969 to 3.07 in 1980–1987. $\mathrm{mTL_c}$ values were calculated as 3.10 and 3.033 in the periods 1988–1994 and 1995–2000, respectively. Furthermore, the catches by trophic levels showed that different trophic levels dominated the fishery catches in the particular periods (Table 9). In period 1960–1969, TL III and TL IV constituted 64% and 35% of the entire fishery yield in the system, respectively. In 1980–1987, the percentage of TL IV organisms in fishery catches decreased to 7.8%, whereas TL III species constituted 90% of the yield. In 1988–1994, the catch composition comprised 82% of TL III groups and 12.6% of TL IV groups. In 1995–2000, the percentage of TL IV organisms in the catches decreased to 4.5%, whereas the percentage of TL III organisms increased to 92%. Similarly, the biomass distribution by trophic levels in the system reflected the dominance of different trophic level species in the four model periods (Table 10). The ecosystem was dominated by TL IV and TL III organisms which represented 64.5% and 35% of all biomasses, respectively, in 1960–1969, illustrating the dominance of higher-trophic-level groups within the ecosystem. In 1980–1987, TL III organisms comprised over 90% of the total biomass within the ecosystem, whereas the percentage of TL IV organisms decreased to 7.7%. This showed the impact of removing top predatory species from the ecosystem by fisheries. The percentage of TL IV organisms in the total living biomass increased to 12.5% when TL III organisms decreased to 83% in period 1988–1994. This was a direct consequence of the collapse of small pelagic fish stocks, which in turn, was reflected as an increase in the relative biomass contribution of higher-trophic-level species in the community. In the final period (1995–2000), the proportion of TL IV organisms decreased to 5% and the percentage of TL III organisms increased to 92% because of the recovery of the small pelagic fish stocks.

Finn's Cycling Index (FCI) decreased from 9.4% in 1960–1969 to 4.61% in 1980–1987. It further decreased down to 2.76% in 1988–1994. This indicated that nutrient turnover in the food-web increased from 1960–1969 to 1980–1987 and 1988–1994. The FCI increased to 15.01% in 1995–2000 because of a slight ecosystem-wide recovery, i.e., improving transfer efficiency rates of trophic flows through the food web and reduction in the proportion of the short-circuited energy flows, in response to the reduced eutrophication and the introduction of the *Mnemiopsis*–predator *Beroe*. This impact was also reflected in the Finn's mean path length which was calculated as 2.662, 2.477, and 2.320 in 1960–1969, 1980–1987, and 1988–1994, respectively, showing a shortening in the average distance of a unit of energy travelled within the food web as the system degraded (i.e., short-circuiting of energy flows) in 1980–1987 and 1988–1994. A subsequent increase in Finn's mean path length to 2.936 in 1995–2000 was consistent with the slight recovery that was observed in ecosystem conditions.

The biomass ratios of *Aurelia*, *Mnemiopsis* and *Noctiluca*, which could be considered as r-strategist species, to the community biomass in general and plankton biomass in particular, increased from 0.0435 in 1960–1969 to 0.347 and 0.633 in 1980–1987 and 1988–1994, respectively. This reflected the increased perturbations, i.e., stress conditions sensu Odum (1985), which prevailed in the Black Sea ecosystem during these latter periods.

4. Discussions and conclusions

4.1. Considerations specific to the methodology

Although the present study utilised some parameterisations of previous mass-balance modelling studies in the Black Sea, it elaborated these former contributions by including further parameter adjustments and model currency changes by incorporating previously neglected but ecologically important food web organisms, and by discriminating between the opportunistic organisms adversely affecting the food web conditions. Furthermore, our study focused more on the ecosystem functioning itself through energetic flows and prey–predator interactions with the help of synthetically produced trophic indicators. These aspects of the study allowed us to fill some gaps in understanding the

Table 9
Catches by trophic levels in four modelled periods of the Black Sea.

Trophic level	1960–1969	1980–1987	1988–1994	1995–2000
V	0.00004	0.00004	0.00004	0.00004
IV	0.0109	0.0355	0.0266	0.0133
III	0.02	0.415	0.175	0.249
II	0	0.00824	0.00937	0.00614
I	0	0	0	0

Table 10
Living biomass by trophic levels in four modelled periods of the Black Sea.

Trophic level	1960–1969	1980–1987	1988–1994	1995–2000
V	0.0004	0.0004	0.0004	0.0004
IV	0.0487	0.187	0.0878	0.0558
III	0.24	1.929	1.142	0.8
II	0.771	2.172	1.679	1.817
I	0.88	1.95	1.95	1.194

changes the Black Sea ecosystem had undergone in the second half of the 20th century.

The simplicity of the model scheme, i.e., the inclusion of a limited number of functional groups, was designed purposefully to not overcomplicate the models to cause an increasing source of uncertainty in the model outputs because of the increased number of parameters required to set up the models. However, our modelling scheme was capable of adequately representing the general structure of the Black Sea food web to derive interpretations from ecological indicators that were calculated utilising the food web's functional properties. It was more of a concern for this study to examine the characteristics of the food web over the model periods by focusing on traits of organisms rather than dealing with specific species dynamics within the ecosystem.

In our study, it was assumed that the *EE* values that were calculated by the mass-balance model set-up in the first period for dolphins and pelagic piscivorous fish groups of the Black Sea would approximately remain unchanged in the latter model periods. This assumption might have impacted the calculated values of indicators, such as keystoneness for these groups. However, considering the complete absence of stock assessment studies for these two functional groups, this assumption was inevitable. Furthermore, the exploitation levels of pelagic piscivorous fish should have remained approximately stable over the years if the high fishery demand on these fishes was acknowledged (Gucu, 2002; Oguz, 2007; Oguz et al., 2008), hence leading to the high *EE* estimates used in this work. Pelagic piscivorous fish in the Black Sea has always been under exceeding levels of exploitation and their predators have been limited in the system. Hence, it could be assumed that *EE* values for this functional group might have fluctuated around the same mean value over the four modelled periods. However, dolphins had been exploited intensively in the Black Sea until the ban of its fisheries in 1966 in the USSR, Bulgaria and Romania and finally in 1983 in Turkey (Birkun, 2008). Therefore, a decreasing *EE* value was most likely to be expected for the dolphins group over the four modelled periods. In this aspect, it could be stated that our model set-ups led to relatively higher estimates of natural mortality values for this group. However, by-catch has been a significant source of mortality for dolphins even after the dolphin fishery ban in the Black Sea (2000–3000 individuals per year, Ozturk et al., 1999), which might have compensated for the release of fishing pressure on this group after the fishing bans causing high “natural” mortality levels.

4.2. Interpretation of model results

The present study provided an assessment of the Black Sea ecosystem structure and function using the ecological indicators approach pioneered by Odum (1969, 1985) and elaborated upon by many others (Christensen, 1995; Costanza and Mageau, 1999; Gaichas et al., 2009; Shannon et al., 2009; Ulanowicz, 2004; Ulanowicz and Puccia, 1990). A similar approach with limited scope was previously implemented in the Black Sea by Christensen and Caddy (1993) that compared the pre-*Mnemiopsis* (early 1980s) and post-*Mnemiopsis* (early 1990s) periods and examined the likely impacts of *B. ovata* on the *Mnemiopsis* population. Our work expanded upon this in terms of analysis complexity and time periods of the examined ecosystem. Our study differed from those of Gucu (2002) and Daskalov (2002) on the interpretation of model products because this study comprised the entire food-web and its quantitative analysis with ecological indicators to assess the ecosystem status that prevailed in the Black Sea during the last few decades.

Evidence of top-down control in the first period (1960–1969) was demonstrated by the highest KS value belonging to the dolphins group in the food web. Considering that food webs are under the tension of either top-down/bottom-up or wasp-waist controls in terms of trophic relationships, predator keystone species could be interpreted as exerting top-down control on their food web. Similarly, low trophic level groups ranking high in terms of keystoneness highlight the important role of their primary or secondary production in shaping the food web. One other interesting outcome of our analysis was the lack of recovery of dolphins, even though the dolphin fishery was banned after 1966 in the USSR, Bulgaria, Romania and 1983 in Turkey. This was clearly supported by the MTI and transfer efficiency (TE) analyses. In the MTI analysis, the continuous increase in the negative impact of fisheries on dolphins even after the fishing ban suggested that excessive harvesting of small and large pelagic fish did not leave sufficient food resources for dolphins to promote their population growth, and hence, consolidated the indirect negative impact of fisheries on dolphins. TE analysis further quantified increasing resource supply to TL II consistent with intensive eutrophication, but this did not propagate further up the food web because of the short-circuiting of energy flows by the gelatinous population that dominated the TLs II–III. This short-circuiting and the decrease in energy transfer efficiency to higher trophic levels were also signified by the decrease in Finn's Cycling and Finn's mean path length indicators starting from the first period. Further evidence for the severity of this short-circuiting effect was provided by the KS value of *Mnemiopsis* in 1988–1994, which suggested *Mnemiopsis* was the second most significant keystone species after the zooplankton group.

The impact of intensive eutrophication was also reflected in the TST values of the ecosystem which increased almost two-fold between the first and second model periods. This reversal in the food web from a top-down controlled state to become more influenced by bottom-up controls was demonstrated by the highest keystone values that were calculated for zooplankton and phytoplankton groups in the latter three model periods. Fisheries also played an important role in this reorganisation as depicted by the decrease in the mean trophic level of the catch ($\mathrm{mTL_c}$) and the mean trophic level of community ($\mathrm{mTL_{co}}$) indices because of selective extraction of particular fish groups from the ecosystem so that top-down control on the food web abated. This “fishing down the food web” (Pauly et al., 1998) impact has been continuing in the Black Sea since the 1960s.

Consistent with Odum (1985), the patterns of many ecological indicators revealed that the Black Sea ecosystem underwent stressed conditions in the final periods examined. The net system production, an indicator expected to be close to zero in mature ecosystems, increased roughly three-fold from the first period to the latter two periods. Similarly, the TPP/TR ratio increased approximately four-fold from a close-to-unity value (typical for healthy ecosystems) in the first time period to the subsequent time periods, also suggesting this deterioration (growing instability) in the ecosystem. The biomass ratio of the sum of opportunistic species *Mnemiopsis*, *Aurelia*, and *Noctiluca* with respect to the total zooplankton increased by more than an order of magnitude from the first period to 1988–1994. These species had no natural predators within the Black Sea ecosystem. Hence, the accumulated energy in the respective TLs of these organisms was not transferred upwards in the trophic chain but circuited back to detritus by natural mortality. This leakage in the food web reduced the TE of flows through the trophic chain to TL III and above (Fig. 5).

In conclusion, contrary to Gucu (2002) and Daskalov (2002) who suggested overfishing as the prime cause of the collapse of small pelagic fish stocks in 1989, we conclude that according to our analyses this collapse was most likely related to more than one single cause. Indeed, overexploitation by fisheries was severe and evident in the various system indices, such as i) the decrease in the mean trophic level of the catches from 3.34 in 1960–1969 down to 3.07 in 1980–1987, ii) the increase in primary production required to support catches from 6.87% in 1960–1969 to 52.82% in 1980–1987, and iii) the increase in the proportion of opportunistic species within the plankton community. However, the increased competition between gelatinous organisms and small pelagic fish for resources represents an additional explanation for the fish collapse that is supported by our results. In fact, the MTI analysis estimated increasing negative impact index values between gelatinous

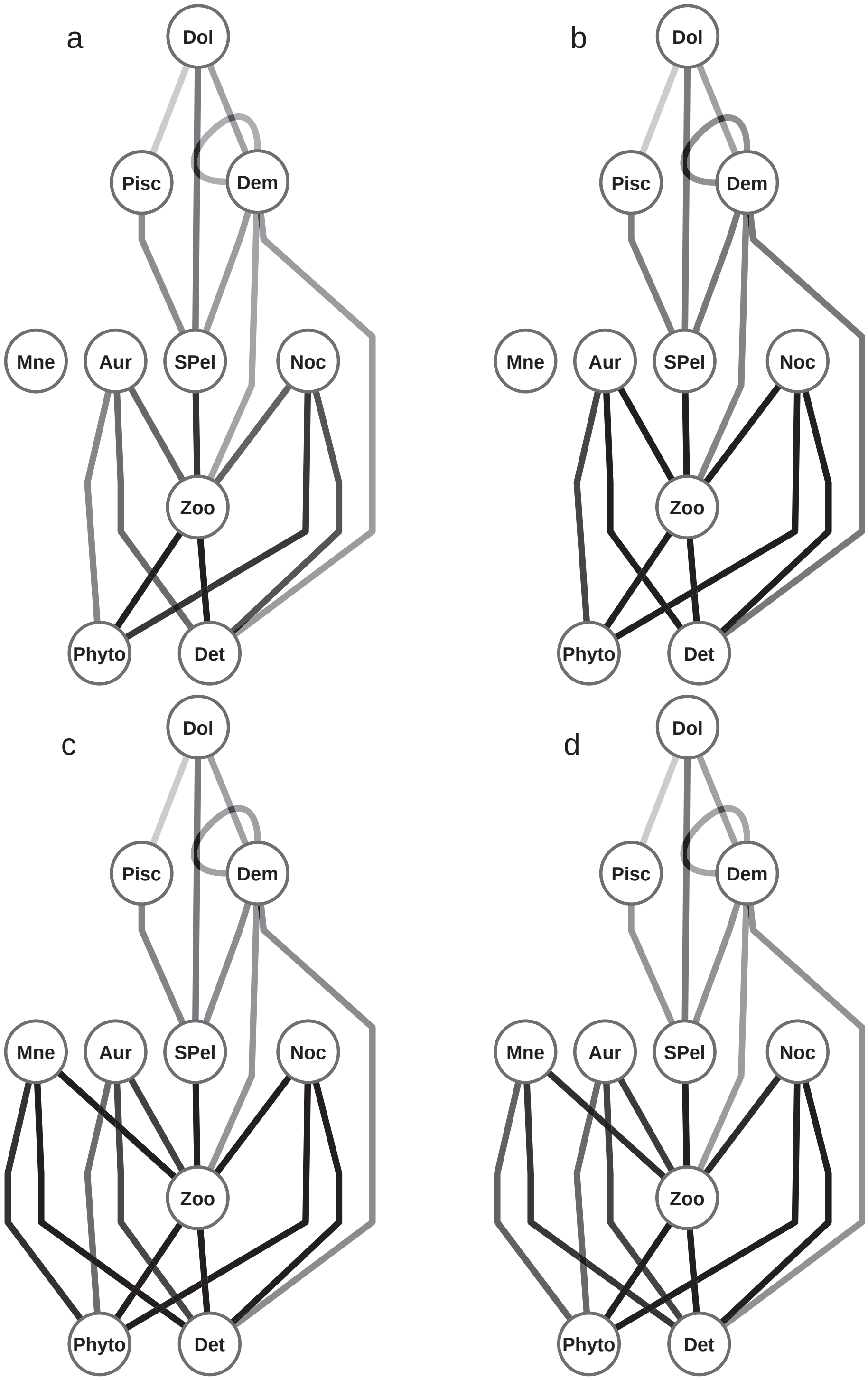

Fig. 5. Trophic flows between the model compartments in periods a) 1960–1969, b) 1980–1987, c) 1988–1994 and d) 1995–2000. The opacity of the lines is proportional to the flow magnitude and normalised across different periods. Special attention should be given to the consolidation of flows within the lower-trophic-level compartment along with the increase in flows in 1980–1987 and the proliferation of alien comb jelly *Mnemiopsis* in 1988–1994. The path length of the flows cycled within the system from period 1960–1969 to other periods decreased as the flows were trapped down in the lower-trophic-level compartments of the food web. The introduction of the alien comb jelly further branched lower-trophic-level flows in three new pathways. Abbreviations: Dol (dolphins), Pisc (pelagic piscivorous fish), Dem (demersal fish), SPel (small pelagic fish), Aur (*Aurelia*), Mne (*Mnemiopsis*), Noc (*Noctiluca*), Zoo (zooplankton), Phyto (phytoplankton), Det (detritus).

organisms and small pelagic fish groups in the last two periods. The trophic competition between *Aurelia* and small pelagic fish in 1980–1987 (negative MTI) was further exacerbated by the proliferation of *Mnemiopsis* as shown by the strong negative impact between *Mnemiopsis* and small pelagic fish in 1988–1994. Based on the ecological indicators and statistical properties of the Black Sea ecosystem that was examined in our work, we propose that the synergistic effects of "resource competition" with jellyfish and "overexploitation" by fisheries were the most likely causes to lead such a collapse in the small pelagic fish stocks in 1989.

A better understanding of the roles played by ecosystem drivers and key species is vital for future ecosystem management of the Black Sea in the face of continuous anthropogenic pressures and climatic change. In this regard, using the Black Sea ecosystem as a case study, our work showed that the structure and function of a marine ecosystem can be examined coherently through a carefully selected set of ecological indicators that can help highlight the main drivers and causes of changes. A time-dynamic Ecosim model of the Black Sea with application of network analyses to obtain dynamically varying ecological indicators would, possibly, further complement the findings of this work. Nevertheless, the advantage of this study is that relevant insights were obtained with a simple but quantitative approach, allowing the assessment of the Black Sea's food web structure and function over the last few decades from a parsimonious set of parameters. This application, therefore, allowed us to provide a baseline towards establishing the goal of “integrated ecosystem assessment” (Levin et al., 2009) for the region.

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