

Overfishing drives a trophic cascade in the Black Sea

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ABSTRACT: During recent decades, environmental conditions have deteriorated in the Black Sea. Population explosions of phytoplankton and jellyfish have become frequent and several fish stocks have collapsed. In this study, literature sources and long-term data are explored in order to find empirical evidence for ecosystem effects of fishing. Inverse trends of decreasing predators, increasing planktivorous fish, decreasing zooplankton and increasing phytoplankton biomass are revealed. Increased phytoplankton biomass provoked decreasing transparency and nutrient content in surface water. A massive development of jellyfish during the 1970s and 1980s had a great impact on consumption and consequent decrease in zooplankton. The turning point for these changes occurred in the early 1970s, when industrial fishing started and stocks of pelagic predators (bonito, mackerel, bluefish, dolphins) became severely depleted. A 'trophic cascade' is invoked as a mechanism to explain observed changes. According to this hypothesis, reduction in apex predators decreases consumer control and leads to higher abundance of planktivorous fish. The increased consumption by planktivorous fish causes a consequent decline in zooplankton biomass, which reduces grazing pressure on phytoplankton and allows its standing crop to increase. The effects of fishing and eutrophication are explored using a dynamic mass-balance model. A balanced model is built using 15 ecological groups including bacteria, phytoplankton, zooplankton, protozoa, ctenophores, medusae, chaetognaths, fishes and dolphins. Ecosystem dynamics are simulated over 30 yr, assuming alternative scenarios of increasing fishing pressure and eutrophication. The changes in simulated biomass are similar in direction and magnitude to observed data from long-term monitoring. The cascade pattern is explained by the removal of predators and its effect on trophic interactions, while the inclusion of eutrophication effects leads to biomass increase in all groups. The present study demonstrates that the combination of uncontrolled fisheries and eutrophication can cause important alterations in the structure and dynamics of a large marine ecosystem. These findings may provide insights for ecosystem management, suggesting that conserving and restoring natural stocks of fish and marine mammals can contribute greatly to sustaining viable marine ecosystems.

KEY WORDS: Trophic cascade · Food-web control · Overfishing · Predation · Eutrophication · Blooms · Black Sea

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INTRODUCTION

During recent decades, environmental conditions have deteriorated in the Black Sea. Population explosions of phytoplankton and jellyfish have become more

frequent and several fish stocks have collapsed (Caddy & Griffiths 1990, Zaitsev 1993, Prodanov et al. 1997). Shifts in seawater quality and fisheries landings were accompanied by modifications in species diversity, and structure of marine communities (Gomoiu 1985, Zaitsev & Mamaev 1997). Stocks of top predators were severely depleted during the 1950s and 1960s and the stocks of small planktivorous fish subsequently increased. By the late 1980s, an already unfavourable

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Table 1. Sources of data used in long-term data analyses and mass-balance modelling

Data	Source
Phosphate content	Bryantsev et al. (1985)
Phytoplankton	Petipa et al. (1970), Kondratieva (1979), Prodanov et al. (1997), Velikova (1998)
Zooplankton	Petipa et al. (1970), Grese (1979b), Shushkina et al. (1983), Prodanov et al. (1997)
Protozoan	Shushkina et al. (1983), Shushkina & Vinogradov (1991)
<i>Noctiluca scintillans</i>	Grese (1979a), Simonov et al. (1992)
<i>Pleurobrachia pileus</i>	Grese (1979b), Simonov et al. (1992)
<i>Aurelia aurita</i>	Mironov (1971), Grese (1979b), Shushkina & Musaeva (1983), Prodanov et al. (1997)
<i>Sagitta setosa</i>	Grese (1979b), Mashtakova (1985), Shushkina & Vinogradov (1991)
Fish larvae	Dehknik (1979), Tkatcheva & Benko (1979)
Fish	Tkatcheva & Benko (1979), Ivanov & Beverton (1985), Shul'man & Urdenko (1989), Prodanov et al. (1997), Daskalov (1998)
Dolphins	Vodyanitzkiy (1954), Sirotenko et al. (1979), Özturk (1996)

ecological situation was exacerbated by the coincident invasion of an exotic ctenophore, *Mnemiopsis leidyi*, and there was a severe collapse in fisheries.

The complex dynamics of bottom-up (resource limitation) and top-down (consumer control) interactions regulate natural communities (McQueen et al. 1986, Hunter & Price 1992, Verity & Smetacek 1996). According to the bottom-up approach, organisms on each trophic level are resource-limited and their population abundance depends mainly on the availability of their food (or nutrients for plants). The top-down view focuses on control of prey dynamics by predators; only the top predators experience resource limitation, and they regulate the abundance of their prey. At each successive, lower trophic level, populations are alternately either resource- or predator-regulated (Fretwell 1977). Thus, the impact of top predators may propagate down the food web, influencing lower trophic levels and ultimately regulating primary production through a trophic cascade (Carpenter et al. 1985).

Although the bottom-up approach is traditional in oceanography, the top-down view has been favoured in terrestrial ecology (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981) and limnology (Hrbaček et al. 1961, Carpenter et al. 1985, Northcote 1988).

Most of the work on top-down effects and trophic cascades has been carried out in freshwater ecosystems, mainly relatively small lakes (e.g. Carpenter & Kitchell 1988, Persson et al. 1992, Carpenter & Kitchell 1993). Examples of top-down effects can be found in studies of marine littoral communities (Paine 1992, Menge et al. 1994, Estes & Duggins 1995). Many of these works are based on results from ecosystem experiments. The scientific knowledge on trophic interactions has been applied in lake management using so-called 'biomanipulation' (Shapiro et al. 1975, Hansson et al. 1998). Attempts have been made to explain large marine systems exploited by fisheries as being regulated by top-down or bottom-up processes (e.g. Skud 1982, Kozlow 1983, Rudsdam et al. 1994, Parsons 1996). In most cases,

Table 2. Input values and results from the mass-balance model of the pelagic food web in the 1960s. Alternative entries for the 'Fishing & Eutrophication 2' scenario are in **bold**. Flows are in $\text{gC m}^{-2} \text{yr}^{-1}$ and rates are on an annual basis. *P/B*: relative production; *Q/B*: consumption/biomass ratio; *EE*: ecotrophic efficiency

Groups	Biomass	<i>P/B</i>	<i>Q/B</i>	Harvest	<i>EE</i>	Fishing mortality
Small phytoplankton	0.20	<u>526.30</u>			0.98	
Large phytoplankton	0.68	223.00			<u>0.67</u>	
Protozoan	0.17	160.00	584.00		<u>0.93</u>	
Small zooplankton	0.20	<u>65.48</u>	420.00		0.98	
Large zooplankton	0.46	34.40	312.86		<u>0.29</u>	
<i>Noctiluca scintillans</i>	0.09	7.30	36.20		<u>0.00</u>	
<i>Pleurobrachia pileus</i>	0.02	10.95/ 20.00	29.20/ 100.00		<u>0.02/0.17</u>	
<i>Aurelia aurita</i>	0.03	10.95/ 20.00	29.20/ 100.00		<u>0.00</u>	
<i>Sagitta setosa</i>	0.08	36.50/ 40.00	73.00/ 110.00		<u>0.29/0.26</u>	
Fish larvae	0.01	5.00/ 5.20	20.00		<u>0.53/0.98</u>	
Planktivorous fish	0.19	<u>1.53/2.00</u>	10.99/ 20.00	0.02	0.98/ 0.77	0.13
Demersal fish	0.05	<u>0.63</u>	1.50	0.00	0.98	0.02
Pelagic piscivores	0.02	0.55	5.00	0.01	<u>0.99</u>	0.29
Dolphins	0.01	0.35	19.00	0.00	<u>0.57</u>	0.20
Detritus	<u>82.53</u>	–	–		<u>0.67/0.68</u>	

mackerel, bonito and bluefish in the 'pelagic predators' compartment, and whiting and spiny dogfish in the 'demersal fish' compartment.

The Ecopath model assumes a mass-balance over a certain period (usually 1 yr). The model is parameterised based on 2 general equations (Christensen et al. 2000). The first describes the production rate of each ecological group over the period as a sum of the rates of biomass accumulation, net migration (emigration minus immigration), fishery catch, predation mortality and other mortality due to disease, old age etc.:

$$\text{Production} = \text{biomass accumulation} + \text{net migration} + \text{fishery catch} + \text{predation mortality} + \text{other mortality} \quad (1)$$

The second equation expresses the energy balance of the group:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

The formal expression of these equations, as well as an explicit form of the system of linear equations describing the modelled ecosystem are given by Christensen et al. (2000) and are available at: www.ecopath.org.

The main input parameters are the biomass (B), relative production (P/B), consumption:biomass ratio (Q/B) and ecotrophic efficiency (EE) of all groups; if one of the parameters is unknown for a group, then the model can estimate it. EE is the fraction of the production of each group that is used in the system. P/B is assumed to be equivalent to total mortality (Z , Allen 1971), which is the sum of all mortality due to fishing, predation, diseases etc. Additionally, catches, assimilation, migration and biomass accumulation rates, as well as diet composition for all groups (Tables 2 & 3) are required as inputs. A system of n linear equations for n groups is solved, in order to quantify the biomass flows in the system and to estimate the missing parameters. The 'detritus' group is formed as a model output from the 'flows to detritus' of all living groups, consisting of the non-assimilated fraction of the food and the losses due to 'other mortality'.

In the temporal dynamic model 'Ecosim' (Walters et al. 1997), a set of coupled differential equations is derived from the Ecopath linear equations in the form:

$$dB_i/dt = g_i \sum C_{ji} - \sum C_{ij} - I_i - (M_i + F_i + E_i)B_i$$

where dB_i/dt is the biomass growth rate of group i during the time interval dt , g_i is the growth efficiency, M_i , F_i , I_i and E_i are the natural mortality, fishing mortality, immigration and emigration rates respectively, and C_{ji} , C_{ij} are consumption rates. $\sum C_{ji}$ expresses the total consumption by group i , and $\sum C_{ij}$ is the predation on group i by all its predators. The consumption rates are calculated by assuming that prey biomass consists of

vulnerable and invulnerable components, and the transfer rate (v_{ij}) between these components determines whether the control is predominantly top-down (Lotka-Volterra dynamics) or bottom-up (resource limitation). The vulnerability v_{ij} are scaled in such a manner that the user can specify values from 0 for bottom-up control, to 1 for top-down control. In this study, top-down control was assumed and all v_{ij} were set to 0.9, except for *Noctiluca* and fish larvae where 'mixed control' $v_{ij} = 0.5$ was assumed.

The Ecosim model was used to simulate the temporal evolution of biomass for the groups included, in response to changes in fishing intensity and eutrophication. In order to run Ecosim simulations, fishing mortality patterns over time must be specified for all fishable components. Allowing an increase in primary production as a forcing function can simulate the effect of eutrophication.

RESULTS

Key trends and events relating to top-down effects

Time series of piscivorous and planktivorous fish, zooplankton and phytoplankton, and phosphate content in surface water are plotted in Fig. 1. Inverse trends can be interpreted in the light of the trophic cascade hypothesis. The turning point in the observed changes occurs in the early 1970s, when the stocks of pelagic predators were severely depleted. Spearman rank correlation is estimated for pairs of log-transformed original series shown on Fig. 1. The highly significant negative correlation between time-series is mainly due to the inverse trends, rather than to yearly variations. Other important events attributable to top-down effects are summarised in Table 4.

In the late 1960s, predator control of small planktivorous fishes (i.e. sprat, anchovy, horse mackerel) decreased to a great extent. The large dolphin population, which consumed about 500 000 t of fish (mostly sprat and anchovy), was diminished ca 10-fold due to overexploitation (Sirotenko et al 1979, Öztürk 1996). Because of the great reduction in stocks, the dolphin fishery was stopped in Bulgaria, Romania and the former USSR in 1966, but continued in Turkey until 1983. Before 1970, fishery landings were dominated by large, valuable migratory species, the most abundant being the bonito *Sarda sarda* followed by the Black Sea mackerel *Scomber scombrus* and the bluefish *Pomatomus saltator*. Large migratory predators such as bluefin tuna and swordfish were also regularly reported in catch statistics. A larger morp of the horse mackerel *Trachurus mediterraneus* existed in the Black Sea, and was caught in considerable quantities

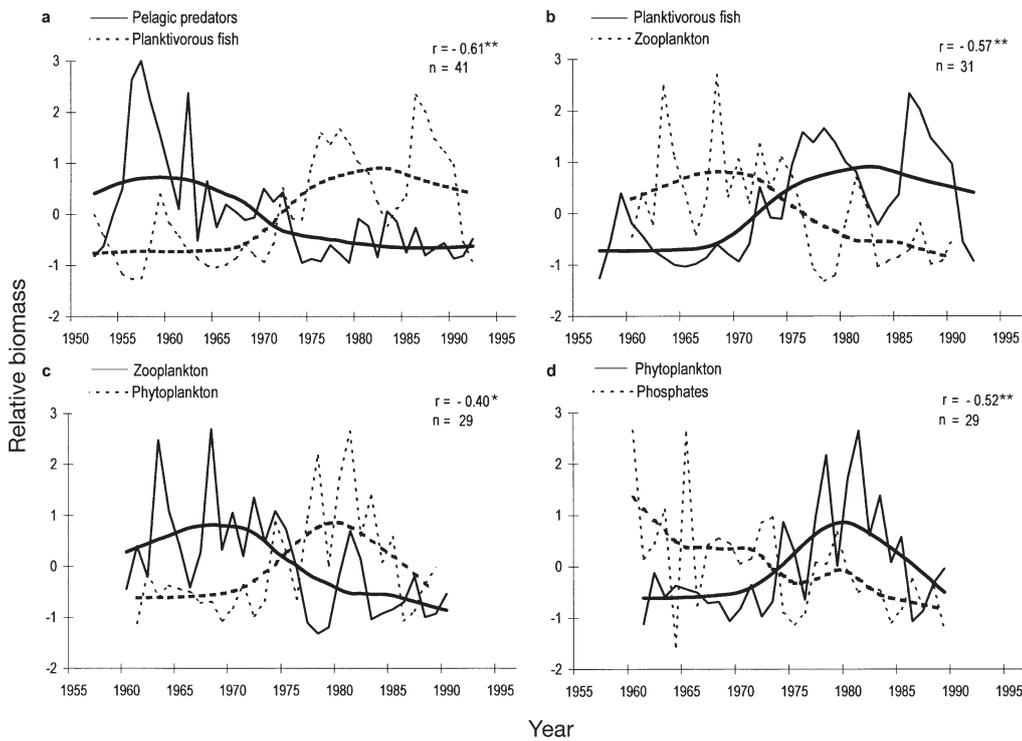


Fig. 1. Inverse trends across consecutive trophic levels. Light curves give original data (subtracting the mean and dividing by the variance), bold curves give non-linear trends smoothed by locally weighted regression (loess). (a) Pelagic predatory fish (bonito, mackerel, bluefish) catch versus planktivorous fish (sprat, horse mackerel) biomass, (b) planktivorous fish biomass versus zooplankton biomass, (c) zooplankton biomass versus phytoplankton biomass, (d) phytoplankton biomass versus phosphate content in surface water. Spearman rank correlation is estimated for pairs of log-transformed original series given on each panel. Correlation coefficients (r) are significant at $**p < 0.01$ and $*p < 0.05$

Table 4. Major trends and events in the Black Sea ecosystem and fisheries before and after 1970

Before 1970	After 1970
Abundant stocks and operating fishery on dolphins	Low dolphin stocks, fishery stopped
High relative abundance of large pelagic predatory fishes (tuna, swordfish, large bonito) in catches	No large pelagic predators reported in catches from the northern Black Sea
Regular migration and abundance of bonito and bluefish	Collapse of bonito and bluefish stocks and fisheries followed by their partial recovery in the southern Black Sea
Regular migration and abundance of the mackerel <i>Scomber scombrus</i>	Disappearance of the mackerel <i>Scomber scombrus</i> from the northern Black Sea
Stock and fishery for large horse mackerel	No catches of large horse mackerel
Moderate standing stocks of small pelagics (important as food for predators)	Increase in the standing stocks of small pelagics that form the basis of an industrial fishery
High diversity of exploited fishes with dominance of large valuable species	Low diversity of exploited fishes with dominance of small pelagics
Relatively low abundance of gelatinous plankton	Blooms of the gelatinous plankton including invaders such as <i>Mnemiopsis</i> and <i>Beroe</i>
Relatively high zooplankton biomass and moderate	Relatively low zooplankton biomass, high phytoplankton biomass producing frequent and intense blooms, structural changes in plankton community composition
High water transparency	Decrease in water transparency causing a dramatic reduction of the red algae <i>Phyllophora</i> in the northwestern Black Sea
High oxygen content in bottom waters of shelf	Decrease in oxygen content causing hypoxia and degradation of benthic communities
High phosphate and silicate contents in surface water	Decrease in phosphate and silicate contents in surface water

during the 1950s and 1960s. By the late 1960s all of these important fisheries had collapsed, mainly due to heavy unregulated fishing. The large variety of horse mackerel disappeared from the Black Sea and the mackerel also moved from its main area of distribution in the northern and western Black Sea; the stocks never recovered. The bonito and bluefish stocks were severely depleted (Fig. 1a). In the early 1970s the stocks of planktivorous fishes increased considerably and became a target for an industrial fishery. In the mid 1980s the total catch reached near 10^6 t, about 65% of which was anchovy and about 20% consisted of sprat and a smaller variety of horse mackerel (Prodanov et al. 1997). The consumption of zooplankton obviously increased; moreover, during the 1970s and 1980s the jellyfish biomass increased considerably. A dramatic increase of the large scyphozoan *Rhizostoma pulmo* was observed in the early 1970s (Zaitzev & Mamaev 1997) and another species, *Aurelia aurita*, became dominant in the early 1980s, its biomass reaching $>1 \text{ kg m}^{-2}$ (Shushkina & Musaeva 1983). By the late 1980s *Aurelia* was replaced in the dominant position by the exotic ctenophore *Mnemiopsis leydyi*, which developed in similar quantities ($\sim 2 \text{ kg m}^{-2}$ or 7.0×10^{-8} t, Shushkina & Vinogradov 1991). As a consequence, the zooplankton biomass decreased ca 2-fold compared with the 1960s (Fig. 1b). This reduced the grazing pressure on phytoplankton and the standing crop doubled during the 1980s (Fig. 1c). The increase in phytoplankton biomass resulted in increased pumping of nutrients and their reduction in the surface layer since 1975 (Fig. 1d). The frequent phytoplankton blooms and the bulk of unutilized algal biomass produced a shift in the water quality to a state characterized by low transparency and high production of detritus, causing oxygen depletion and hypoxia near the bottom. Benthic mortality under low oxygen conditions acted as a feedback, amplifying the situation. The mortality of the stocks of mussels and other benthic filter-feeders allowed the increase in unutilized detritus, causing oxygen depletion.

Most of these events have been interpreted in the light of the bottom-up approach, referring to anthropogenic eutrophication as a main causative factor.

Table 5. Change in dominance across the pelagic food chain since the depletion of top-predators after 1970

Trophic level	Before 1970	After 1970
Top predators	Resource limited	–
Planktivores	Consumer controlled	Resource limited
Zooplankton	Resource limited	Consumer controlled
Phytoplankton	Consumer controlled	Resource limited

There is no doubt about the impact of eutrophication on many of the processes in the sea, but community variation in response to the changing environment can also be influenced by top-down forces. Industrial fishing has become the other powerful anthropogenic factor altering natural populations. In Table 5, the hypothetical cascade mechanism is sketched, showing how depletion of the top predators can change the dominance structure of the pelagic food web, leading to alternation of resource limitation and consumer control of successive trophic levels.

Dynamic mass-balance modelling

A mass-balance model of the pelagic food web in the 1960s was constructed (Table 2) and an attempt was made to simulate the observed patterns of biomass dynamics over the next decades. Results from the balanced (Ecopath) model and network analysis are discussed elsewhere (Daskalov 2000). Here I concentrate on the temporal dynamic model.

Several modelling simulations were run in order to explore the effects of fishing and eutrophication (Fig. 2). Firstly, the effects of fishing alone were simulated by assuming a ca 3-fold increase in fishing mortality over 30 yr (Fig. 2a). The fishery forcing on the piscivorous fish and dolphins was handled in such a manner that the changes in biomass predicted by the model correspond to the observed changes. There is no information on the fishing mortality of those predatory groups, but bearing in mind the increasing capacity of the fisheries directed on them (Özturk 1996, Prodanov et al. 1997), the assumed values seem the lowest possible. The increase in fishing mortality of planktivorous and demersal fish corresponds, to estimations by Prodanov et al. (1997) and Daskalov (1998).

The results indicate clear cascade patterns for all ecosystem components (Fig. 2a). Intensive fishing leads to a ca 2-fold decrease in apex predators. As a result of this reduction in predation pressure, the biomass of planktivorous fish increases. The increase in demersal fish biomass is due partly to the decrease of dolphins as direct predators, but in a major extent to the increase of their own main prey, i.e. planktivorous fish. The parallel increase of the invertebrate zooplanktivores *Aurelia* and *Pleurobrachia* seems unexpected, bearing in mind that these species compete with fish for zooplankton food. The critical assumption leading to these results is that planktivorous fish feed in a size-selective manner and consume a dominant proportion of large zooplankton in their diet (Table 3). There is some uncertainty about the food-selectivity of invertebrate zooplanktivores. The local populations of *Aurelia*, *Pleurobrachia* and *Sagitta* are regarded as un-

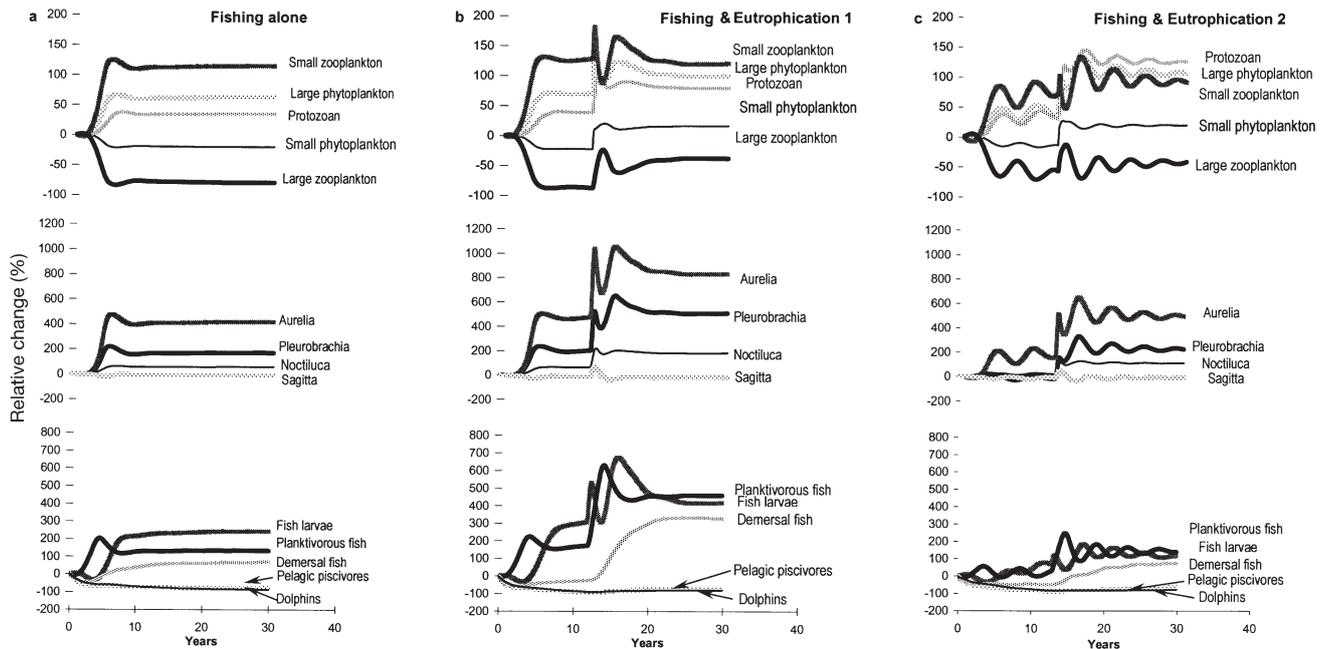


Fig. 2. Results from the temporal dynamic model Ecosim: (a) Changes due to fishing mortality forcing, 'Fishing alone'; (b) Changes due to fishing mortality and eutrophication, 'Fishing & Eutrophication 1'; (c) Same as (b) but using higher P/B and Q/B (see Table 2), 'Fishing & Eutrophication 2'

selective feeders (e.g. Mironov 1971, Sushkina & Musaeva 1983). However, new studies of jellyfish feeding report controversial results, e.g. positive selection for smaller (Costello & Colin 1994, Graham & Kroutil in press) or larger prey (Båmstedt et al 1994, Suchman & Sullivan 1998). Opportunistic feeding was assumed here, resulting in approximately equal proportions of small and large prey in the diets of invertebrate zooplanktivores (Table 3). Model analyses show that results are sensitive to the relative proportions of small versus large prey in the diets of planktivores. This structure in zooplanktivory has an effect on the development of biomass of small and large zooplankton. The elimination of large zooplankton by planktivorous fish allows small zooplankton biomass to increase on a competitive basis, fuelling the growth of the invertebrate zooplanktivore populations. Because of its high P/B , *Sagitta* is an important competitor of the other zooplanktivores, but as a food for fish and *Aurelia* it is controlled from above and its biomass does not change significantly. *Aurelia* has no predators and consumes only a negligible portion of *Pleurobrachia* (Table 3). The increase in biomass of *Aurelia* and *Pleurobrachia* can be explained by the increase in its food: the small zooplankton. As a result, the growing jellyfish populations consume a bigger quantity of large zooplankton that leads to its further decrease. The positive effect on fish larvae can be explained in the same manner, as their food consist of about 60% of

small zooplankton (Table 3). Biomass of protozoa and *Noctiluca* follow the increase in their main food: detritus and phytoplankton. The changes in the zooplankton induce reciprocal changes in phytoplankton that lead to increases in large phytoplankton and decreases in small phytoplankton.

The changes predicted by the 'Fishing alone' scenario fit well to the observed changes between the 1960s and 1980s (Fig. 3). In all groups the direction of the changes is the same as in the observed data (Fig. 3a) and there is less than 0.5% difference in the magnitude of the change (Fig. 3b). The model predicts a decrease in zooplankton and an increase in phytoplankton that is smaller than that observed. As seen from Fig. 2, changes in overall zooplankton and phytoplankton biomass are mainly due to changes in the large-sized fractions of these groups. The changes in small zooplankton and phytoplankton are in opposite directions. Thus the model predicts changes in plankton size structure, with increasing small versus large zooplankton and inversely increasing large versus small phytoplankton. Unfortunately, this prediction cannot be tested directly because of the lack of published size-structured data from the 1980s. However, there is some evidence that such changes in size structure might occur. Velikova (1998) has reported a positive trend in phytoplankton cell volume from 1956 to 1990, with a ca 4-fold increase in cell volume in the 1980s compared to the 1960s. Recent research on spe-

cies and stage structure of copepod populations in relation to the dynamics of the sprat stock has shown a negative correlation between sprat biomass and copepod size, indicating the effect of size-selective consumption by fish (G. Daskalov & V. Mihneva unpubl. data).

That eutrophication was a major factor in the Black Sea during the 1970s and 1980s cannot be ignored when attempting to explain changes in the ecosystem. Alternative scenarios were run, assuming 50% increase in primary production of the 2 phytoplankton groups due to forcing by eutrophication, in order to reproduce the ca 2-fold increase in total phytoplankton biomass. The first run used the same baseline parameters as the 'Fishing alone' scenario and the second one used higher P/B and Q/B coefficients for planktivores, listed in Table 2.

The inclusion of eutrophication does not radically alter the direction of biomass change for the groups (Figs 2 & 3). The primary productivity forcing by 50% led to a >2-fold increase in the biomass of apex predators in the 'Fishing & Eutrophication 1' scenario. As such an increase was not observed in the sea during the 1980s, higher fishing mortality coefficients were applied on the Dolphins and Piscivores groups, in order to fit their biomass to observed values. As a result, stronger direct and indirect effects on lower trophic levels were observed and biomass of planktivorous and demersal fish, and invertebrate zooplanktivores increased substantially beyond the observed values and those simulated by the 'Fishing alone' option (Fig. 3). After some initial perturbation, the small zooplankton biomass stayed on the same level, while large zooplankton biomass increased compared to the 'Fishing alone' option (Fig. 2b). As a result, total zooplankton increased compared to the level in the 1960s, which contradicts the empirical trend (Fig. 3a). Both small and large phytoplankton increased (Fig. 2b) and the total biomass approached the observed level (Fig. 3a). However, the changes simulated by this scenario, as a whole, differed substantially from the observed trends (Fig. 3b).

In the 'Fishing & Eutrophication 2' scenario, higher baseline P/B were assumed to compensate for the effects of increased primary productivity. The new P/B and Q/B coefficients used (Table 2) fall into the range of possible values found in the literature (Table 1). The fluctuations observed in the modelled trends (Fig. 2c)

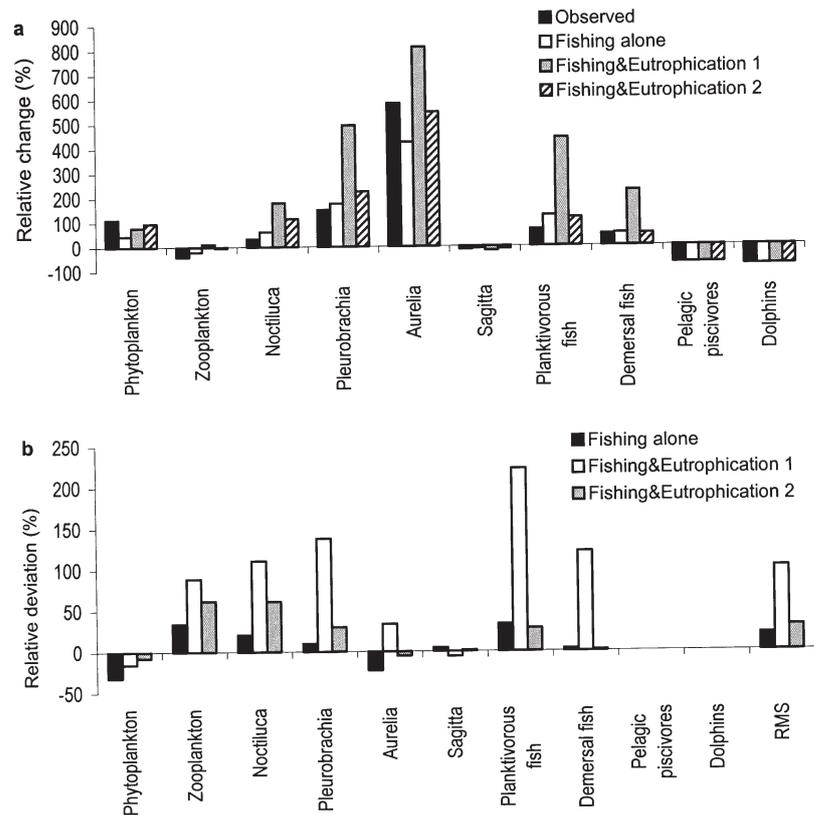


Fig. 3. (a) Percent change between the 1960s and 1980s, in observed and simulated biomass, assuming increasing fishing (Fishing alone), and increasing both fishing and eutrophication (Fishing & Eutrophication 1 & 2). (b) Relative deviation simulated from observed biomass. RMS (root-mean-square) is the square root of the mean of the squares of the deviations of all groups

are due to Lotka-Volterra effects. The results from this scenario are close to the 'Fishing alone' and to the observed trends (Fig. 3). This scenario gives the closest fit to the observed change in phytoplankton biomass (Fig. 3b). The change in zooplankton biomass is not successfully modelled, as only a negligible decrease in total biomass is registered (Fig. 3a). As in the previous 2 scenarios, the decrease in total zooplankton biomass is due to the decrease in large zooplankton. It is also possible that the small zooplankton fraction is under-represented in the observed data, due to the use of a larger mesh size (Shushkina et al. 1983) such that the trend in observed total zooplankton may be representative of the change in the large zooplankton fraction. The relative deviation from the observed data in most of the groups is smaller than with the previous 2 scenarios. The root-mean-square (RMS) of the deviation of all groups, being a measure of the overall deviation, is close to the RMS of 'Fishing alone' and is significantly smaller than the RMS of the 'Fishing & Eutrophication 1' scenario (Fig. 3b).

DISCUSSION

Both overfishing and anthropogenic eutrophication are responsible for the observed changes in the Black Sea ecosystem. However, the results of this study show that top-down effects are more important determinants of ecosystem structure.

Using the modelling experiments, 2 possible explanations have been simulated, i.e. strong or weak top-down effects. The first explains the ecosystem change solely by the action of top-down forces. The fishery eliminated top predators during the 1960s. That led to reduced predation on planktivores, causing their increase during the 1980s; this was followed by cascading zooplankton depression and phytoplankton increase. The 'weak' explanation includes the bottom-up influence of eutrophication as well. It interprets the change as an alteration of respective top-down and bottom-up controls within the food web (Table 5). Phytoplankton and planktivores were mostly resource controlled after 1970. Their abundance was driven by the rise in productivity, while the zooplankton, being consumer controlled, stayed depressed. The first explanation does not seem very likely. It assumes biomass trends independent of the rise in productivity. However, it cannot be tested because productivity did increase after 1970. Both explanations do assume, however, that top-down influence may be exerted through a trophic cascade and therefore become a causal factor for radical structural and functional change in the whole pelagic ecosystem.

The analyses of the structural dynamics of the system revealed possible direct and indirect responses of different groups to top-down and bottom-up forcing. The results indicated the pivotal role of zooplanktivory in the system. Size selective feeding of small pelagic fish is of crucial importance for biomass dynamics of the intermediate and lower trophic levels. It is indirectly responsible for the trends in jellyfishes, which are a primary factor in the consumption of zooplankton. Furthermore, predominant consumption of large zooplankton by fish has pronounced effects on size-structure and biomass trends in zooplankton and phytoplankton. Total zooplankton and phytoplankton biomass are determined mainly by the dynamics of their large size fractions which are more sensitive to top-down effects.

Observed data and modelling results both indicate that changes can be explained by the trophic cascade mechanism. Although such results could be expected if using Lotka-Volterra modelling (as in Koslow 1983, Silvert 1993, 1994) here, they are confirmed by long-term data on 4 trophic levels; that is seldom the case in other large marine ecosystems (e.g. Koslow 1983, Rudsdam et al. 1994, Reid et al. 2000).

A question then arises: are top-down effects more pronounced in the Black Sea than in other large marine ecosystems? It should be noted that the data on which this study is based were collected independently, over more than 3 decades, by different institutions on the eastern and western parts of the sea. These data show consistent trends, but during this time they have mainly been interpreted based on the bottom-up approach. Verity & Smetacek (1996) presented a detailed discussion of why top-down effects are often disregarded in oceanography and of the need to change the paradigm for studying pelagic ecosystems. Another issue that seems to be overlooked by most marine scientists is the effect of industrial fishing. In the case of the Black Sea, natural patterns of abundance and behaviour of predatory fish and dolphins, described in antiquity and persisting over millennia, were suddenly destroyed by uncontrolled exploitation. Certainly, the Black Sea is a quite unique basin and some of its characteristics, such its isolation from the ocean, anoxic deep layer, and relatively low taxonomic diversity, contribute to its high sensitivity to human-induced disturbance. However, the relatively few studies in oceanography and fishery science exploring top-down and trophic-cascade effects do not allow generalisations to be made about the relative importance of bottom-up and top-down processes in different parts of the ocean. It may be that top-down effects are simply easier to detect by means of common observational and experimental approaches in relatively simple ecosystems such as lakes, estuaries, enclosures or low-diversity marine systems, e.g. the Black Sea and the sub-arctic ocean (Skjoldal et al. 1992, Shiomoto et al. 1997). An increasing number of future studies on trophic interactions and the effects of fisheries on different marine ecosystems are expected to restore the balance in understanding the roles of top-down and bottom-up factors in the ocean.

The present study demonstrates that uncontrolled fisheries can cause important alterations in the structure and dynamics of a large marine ecosystem. Since most of the world fisheries are preferentially oriented toward valuable predatory species (Pauly et al. 1998), such effects can also be expected in other areas. These findings may provide insights for ecosystem management, suggesting that conserving and restoring natural stocks of fish and marine mammals through effective fisheries regulation, marine reserves, and other measures, together with water quality and nutrient control, can contribute much to sustaining viable marine ecosystems.

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