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Can Overfishing be Responsible for the Successful Establishment of *Mnemiopsis leidyi* in the Black Sea?

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It is widely known that in 1989 a tremendous biomass of *Mnemiopsis leidyi* was reported in the Black Sea. At the same time, drastic declines in the pelagic fish stocks were reported. Several authors, overlooking the rapid development of the fisheries industry in the Black Sea, pointed out that the new invader was the major factor responsible for the fisheries collapse in the Black Sea. This study examines the development of the Black Sea fisheries industry, along with the ecological changes that were taking place, and evaluates its effect on the ecosystem. A set of balanced steady-state models, corresponding to the periods of the 1960s to 1970s, the 1980s, before the outburst of the *Mnemiopsis leidyi*, and the 1990s, which reflect the present state of the ecosystem, are used to study the successful establishment of the gelatinous organisms in the Black Sea. Using these models, a series of experiments are performed in order to explore the role of each major ecological group within the Black Sea ecosystem at different stages in time over the last 30 years. The budget calculations suggest a minimal role of gelatinous species on the decline of the fish stocks, contrary to the general belief. More interestingly, the model results indicate that the decline in the fish stocks was as a consequence of overfishing and that ever-increasing plankton productivity associated with eutrophication during the 1980s led to the outburst of gelatinous organisms.

Keywords: *Mnemiopsis leidyi*; fisheries ecosystem; energy flow network; Black Sea

Introduction

Over the last few decades, the Black Sea has experienced drastic changes in its ecosystem (Sorokin, 1983; Tolmazin, 1985; Caddy & Griffiths, 1990; Mee, 1992; Zaika, 1992; Niermann *et al.*, 1994) due to the manipulation of river out-flows (Bondar, 1977), changes in nutrient loads (Bologa *et al.*, 1984; Gomoiu, 1990), the introduction of exotic species (Vinogradov *et al.*, 1989; Mutlu *et al.*, 1994) and excessive fishing (Ivanov & Beverton, 1985; Stepnowski *et al.*, 1993; Gucu, 1997).

The main changes of the ecosystem are the domination of some species, especially those adapted to eutrophic conditions, and a decrease in biodiversity (Zaitsev, 1992). The most striking example is the gelatinous carnivores. Among these, the biomass of *Aurelia aurita* has risen with increasing eutrophication of the Black Sea (Caddy & Griffiths, 1990). From 1950–1962, Shushkina and Musayeva (1983) found a biomass in the order of 30 million tons in wet weight. In 1978, a much larger biomass, as large as 400 million tons in wet weight for the whole of the Black Sea, was calculated by Gomoiu (1981). Almost the same figure was given by Flint *et al.* (1989) for the same period.

In 1989, *Mnemiopsis leidyi*, a newly introduced species, appeared in the Black Sea in huge quantities. In the autumn of 1989, a biomass of about 800 million tons wet weight of *M. leidyi* was estimated for the entire Black Sea (Vinogradov, 1990). Its appearance has been synchronously followed by a sudden decline in various fish stocks, and many authors focused on possible predation by *M. leidyi* on pelagic eggs and larvae and sought correspondence with the collapse of the fisheries experienced in 1989 (Vinogradov, 1990; Zaika, 1992). On the other hand, ecosystem modelling (Gucu & Oguz, 1998) suggests that neither the carrying capacity (although increased significantly by the continuous nutrient flow from rivers) nor the trophodynamic structure of the Black Sea support such a high biomass value of *M. leidyi* as that reported in 1989.

The objective of this study was to evaluate fishery development in the Black Sea and analyse the changes in the major fish stocks within the course of the human-induced evolution of the Black Sea ecosystem. For this purpose, the Black Sea history of the last 4–5 decades was evaluated in three ecologically distinguished time periods. First, is the 1960–1970 period of oligotrophy (Sorokin, 1983; Ivanov & Beverton, 1985; Balkas *et al.*, 1990). Second, the period of eutrophy (1978–1988), when increasing

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human population, development in agriculture and industrialization resulted in the increase of nutrient loads to the Black Sea via major European rivers, which turned the Black Sea into one of the most eutrophicated seas of the world (Zaitsev, 1991). Towards the end of the decade, severe changes in the ecosystem took place. Finally, the 1990s, which are considered to be the ' collapse and recovery ' period in recent articles by many authors including Zaitsev and Alexandrov (1997).

On this basis, the trophodynamics of the Black Sea ecosystem have been examined, making use of network analysis (Christensen & Pauly, 1992) designed for each of these three periods.

Materials and methods

Network analysis software description

The ECOPATH 3.0 software (International Center for Living Aquatic Resources Management, Philippines) has been used to estimate the mass flow among different ecosystem components. This model is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984, 1985). Basically, the approach is to model trophic interactions using a set of simultaneous linear equations.

The model assumes the following steady-state balance equation for each biological prey i submitted to the predation of j.

$$B_i(P/B)_i EE_i - \sum_{j=1}^{n} B_j(Q/B)_j DC_{ji} - EX_i = 0 \quad (1)$$

where B_i is the biomass of i; P/B_i is the production/biomass ratio of i; EE_i is the ecotrophic efficiency of i, which corresponds to the fraction of the production that is either predated or exported; B_j is the biomass of predator j; Q/B is the consumption/biomass ratio; DC_{ji} is the fraction of prey i in the average diet of predator j; and EX_i is the export of i.

Based on this, n linear equations can be written for a system with n trophodynamic groups:

$$B_1\, P/B_1\, EE_1 - B_1\, Q/B_1\, DC_{11} - B_2\, Q/B_2\, DC_{21} - \ldots - B_n\, Q/B_n\, DC_{n1} - EX_1 = 0 \quad (2)$$

$$B_2\, P/B_2\, EE_2 - B_1\, Q/B_1\, DC_{12} - B_2\, Q/B_2\, DC_{22} - \ldots - B_n\, Q/B_n\, DC_{n2} - EX_2 = 0 \quad (3)$$

$$\vdots$$

$$B_n\, P/B_n\, EE_n - B_1\, Q/B_1\, DC_{1n} - B_2\, Q/B_2\, DC_{2n} - \ldots - B_n\, Q/B_n\, DC_{nn} - EX_n = 0 \quad (4)$$

This system of equations can be expressed in matrix form as:

$$[A]_{n,m}\,[X]_m = [Q]_m \quad (5)$$

with n being the number of equations and m the number of unknowns.

Given A^{-1} the inverse of the matrix A, this provides:

$$[X]_m = [A^{-1}]_{n,m}\,[Q]_m \quad (6)$$

If the determinant of a matrix is zero, or if the matrix is not square, the program of Mackay (1981) is used to estimate the generalized inverse. If the set of equations is overdetermined (more equations than unknowns), and the equations are not consistent with each other, the generalized inverse method provides least-squares estimates, which minimizes the discrepancies. If, on the other hand, the system is underdetermined (more unknowns than equations), a solution that is still consistent with the data will be output. However, it will not be a unique answer. To optimize the ECOPATH model, a number of algorithms have been included in order to calculate (some of the) missing parameters without using the generalized inverse method (for details of the algorithms see Christensen & Pauly, 1992). However, some requirements must be met for a successful application. Thus, in general, only one of the parameters B, P/B, Q/B or EE may be unknown. The exports and a diet composition matrix are always required. DC, P/B and Q/B are largely determined by the size and food preference of a species. EX is determined by the migratory behaviour and the type of fishery exploiting the species.

For the simplicity of calculation, the species using the same food resource, having the same size and showing similar migratory behaviour were grouped under the same category. On this basis, the Black Sea ecosystem was defined by six trophodynamic components, namely large pelagics, small pelagics, demersals, gelatinous organisms, mezozooplankton, phytoplankton and the harvesters representing fisheries (Table 1). The species included in this table contain the main species inhabiting the Black Sea.

The large pelagics group includes solely migratory piscivorous species. In autumn, they migrate southward to the Marmara and Aegean Seas. The small pelagics are migratory fish as well, but they are small in size and planktivorous. Among them, *Engraulis engrasicolus* and *Trachurus* spp. are the warm-water originated species and they undergo seasonal north–south migration (Rass, 1992). The former species

TABLE 1. Ecosystem structure: trophodynamic groups and main species

Trophodynamic groups	Main species
Large pelagics	*Pomatomus saltator*
	Sarda sarda
	Scomber japonicus
	Scomber scombrus
Demersals	*Merlangius m. euxinus*
	Mullus barbatus poticus
	Psetta maxima
Small pelagics	*Alosa* spp.
	Clupeonella cultriventris
	Engraulis encrasicolus
	Sprattus sprattus
	Trachurus mediterraneus
Gelatinous organisms (jellies)	*Aurelia aurita*
	Mnemiopsis leidyi
	Pleurobrachia pileus
Mesozooplankton	Copepoda
	Chaetognatha
	Cladocera
	Appendicularia
Phytoplankton	Diatoms
	Dinoflagellates
Harvesters	Purse seiners
	Trawlers

remain within the Black Sea and hibernate along the Turkish coast, while the latter emigrates out of the Black Sea via the strait of Bosphorus. *Sprattus sprattus* is a cold-water species and the seasonal movements of the schools are not as pronounced as for warm-water species. *Alosa* spp. and *Clupeonella cultriventris* are of minor importance in the ecosystem, because their population size has always been very small compared to the other small pelagic species.

The gelatinous organisms of the Black Sea are composed of four species of Scyphomedusean and Ctenophora. However, only three of them (*A. aurita*, *M. leidyi* and *Pleurobrachia pileus*, Table 1) were included in the model, because the biomass of the fourth species, *Rhizostoma pulmo*, has never reached significant quantities in the Black Sea. Fodder zooplankton in the Black Sea are grouped as mesozooplankton (Zaitsev & Alexandrov, 1997). Phytoplankton, which is the major food source of the mesozooplankton, is essentially represented by two taxa: diatoms and dinoflagellates (Uysal & Sur, 1995).

Finally, harvesters include two different kinds of fisheries in the flow network: the trawlers and the purse seiners catching the demersals and the pelagics, respectively.

Model application

For a first application, the ECOPATH steady-state model was applied to the 1960s, when the Black Sea was believed to be in a steady-state condition. The biomass B, the parameters P/B, Q/B, EE, and the export EX of Equation 1 were determined for each trophodynamic group on the basis of an analysis of 1955-1965 data (Table 2). It is then assumed that the physiological parameters used in the flow network analysis, such as Q/B, do not differ significantly with the changes taking place in the Black Sea. The same parameters were, therefore, used to run the model for data from the 1980s and 1990s (Table 3).

The unknowns of Tables 2 and 3 were calculated by the model algorithms linking the production of each group with the consumption of all groups, based on the assumption that production from any group

TABLE 2. Input biomass, harvest and parameters taken or calculated from the literature

Group	Biomass ($t\ km^{-2}$)	P/B	Q/B	EE	Harvest ($t\ km^{-2}$)
Large pelagic		1·7[a]	8·7[d]	0·90[g]	0·089[h]
Small pelagic	1·428[a]	2·5[a]	9·0[d]		0·298[h]
Demersal		2·1[a]	12·0[d]	0·90[g]	0·047[h]
Jellies	1·607[b]	10·0[c]	39·2[e]		
Zooplankton	35·000[a]	32·0[c]	137·0[f]		
Phytoplankton	8·806[a]	325·0[c]			

The parameters P/B, Q/B and EE (dimensionless) are as described in Equation 1, and the numbers in superscript indicate the source of the data.
[a]Ivanov and Beverton (1985); [b]Mironov (1971); [c]Greze (1979); [d]Palomares and Pauly (1989); [e]Assuming that the consumption of most groups is about 3–10 times higher than their production, the gross food conversion efficiency (GE), which is defined as the ratio between production and consumption, is set to 0·25. Using the P/B ratio and GE, Q/B is calculated; [f]Petipa, *et al.* (1973); [g]It is assumed that 90% of the fish production is utilized within the ecosystem either by predators or by harvesters; [h]General Fisheries Council of the Mediterranean (GFCM, 1993).

Table 3. Input biomass, parameters and harvest taken or calculated from the literature published for the 1980s and 1990s

Group	Biomass (t km^{-2})	P/B	Q/B	EE	Harvest (t km^{-2})
Large pelagic		1·7	8·7		0·083[h]
Small pelagic (1980s)		3·0[m]	9·0	0·90	1·551[h]
(1990s)					0·238[h]
Demersal	0·351[i]	2·1[m]	12·0		0·088[h]
Jellies (1980s)	952[j]	10·0[e]	39·2		
(1990s)	214[k]				
Zooplankton		32·0	137·0	0·90	
Phytoplankton	340[l]	328·0			

The parameters P/B, Q/B and EE (dimensionless) are as described in Equation 1, and the numbers in superscript indicate the source of the data. Data without superscript are as in Table 2.
[h]General Fisheries Council of the Mediterranean (GFCM, 1993); [i]Bingel *et al.* (1993); [j]Gomoiu (1981); [k]Mutlu *et al.* (1994); [l]Nesterova (1987); [m]Z=P/B (Allen, 1971).

Table 4. Food matrix used in the model

Prey/predator	Large pelagic	Small pelagic	Demersal	Jellies	Zooplankton
Large pelagic	0	0	0	0	0
Small pelagic	0·50	0	0·35	0	0
Demersal	0·10	0	0·10	0	0
Jellies	0	0	0	0	0
Zooplankton	0	1·00	0·20	0·50	0
Phytoplankton	0	0	0	0·10	0·50
Detritus	0	0	0·35	0·40	0·50
Import	0·40	0	0	0	0
Total	1	1	1	1	1

The data of Avsar (1994), Ismen (1995), Slastanenko (1956), Tsikhon-Lukanina and Reznichenko (1991) and Tsikhon-Lukanina *et al.* (1990) were used to compile the food matrix.

has to end somewhere else in a steady-state system. Interrelations between the different ecosystem components were described by a prey/predator matrix (Table 4). An additional import term was added to the matrix of Table 4 in order to take into account the migratory large pelagics (*Sarda sarda*, *Pomatomus saltatrix*) migrating out of the Black Sea through the strait of Bosphorus to the Marmara and Aegean Seas. It is assumed that food requirement during the time period spent outside the Black Sea was fulfilled by an external source. Food assimilation is calculated from ingestion assuming a loss of 20%.

Fisheries data set

The Black Sea anchovy is by far the dominant fish species in the Black Sea and hence reflects, to some extent, the state of the fish stocks. To monitor the changes in the anchovy stocks, the catch of the Turkish fleet was examined between 1985 and 1993. The major landing sites of the purse seines were visited twice a week during the fishing season (November–March) by the Turkish Ministry of Agriculture and Rural Affairs Institute of Fisheries Research, within the framework of the NATO-TU Fisheries project (Bingel *et al.*, 1993). On the each visit, a purse seine was randomly selected and 1–2 kg of fish (100–300 individuals) was sampled from its catch. The total length of anchovies was measured to an accuracy of 0·5 cm. Between November and March, the anchovy migrates to the Turkish coast of the Black Sea to hibernate. The larger individuals arrive at the over-wintering sites first and form a hibernating school before the smaller individuals (Chashchin, 1995). Therefore, there is considerable monthly variation in the length composition of the

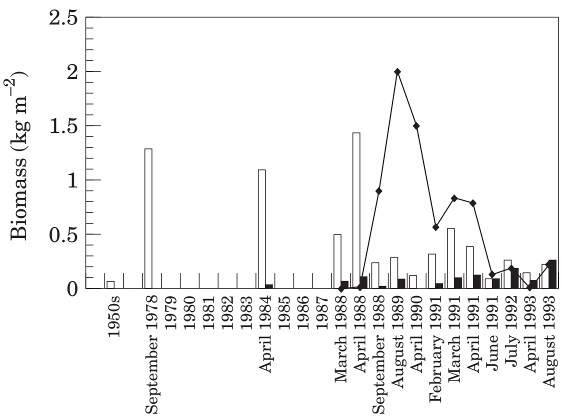

FIGURE 1. Time evolution of the biomass of gelatinous organisms in the Black Sea, estimated at different months (taken from Niermann *et al*., 1994). (□) *Aurelia*; (■) *Pleurobrochia*; (◆) *Mnemiopsis*.

anchovies caught within over-wintering waters. The hibernating anchovies do not feed and hence growth rate slows down remarkably during winter (Chashchin, 1995). The slow winter growth is ignored and monthly samples collected from mid-November to the end of February were added to the same data pool.

Complementary fisheries data of the other Black Sea countries were taken from the Statistical Bulletin for the General Fisheries Council for the Mediterranean (GFCM, 1984, 1993), which is published annually by the Food and Agriculture Organization of the United Nations.

Results and discussion

The 1960s and 1970s

Observations. The most characteristic feature of this period was probably the low phytoplankton biomass, whose average fluctuated around $3{\cdot}6 \times 10^6$ tons for the entire Black Sea (Greze, 1979). This value led to a considerably low annual average mesozooplankton biomass estimate of about $15{\cdot}6 \times 10^6$ tons. The gelatinous organisms were composed of the jellyfish, *A. aurita* only. Mironov (1971) reported 675 000 tons ($1{\cdot}3$ kg m^{-2}) of biomass of *A. aurita* for this period (Figure 1).

As shown by the composition of the fish landing (Table 5), the Black Sea anchovy was the main species in the 1960s catch. The contribution of highly commercial species, such as turbot, mackerel, bluefish and Atlantic bonito, was quite important. Large pelagics are Atlanto–Mediterranean warm-water species. These species migrate between the Black Sea and the Sea of Marmara and the northern Aegean Sea through the Strait of Bosphorus. Among the four species listed in Table 1, only *Sarda sarda* spawn in the Black Sea, while the others lay their eggs in the Marmara or Aegean Sea prior to their northward migration. The mass movement of the fishes takes place in late spring and late autumn (Slastenenko, 1956). During the migration period, the entire stock aggregates in the vicinity of the strait of Bosphorus. They become extremely vulnerable to the fishery while they pass through the strait and are, therefore, heavily exploited by the Turkish fishing fleet. In early 1970s, a sharp

TABLE 5. Distribution (%) and species composition (most common species) of the defined fish compartments in the total landing in the 1960s (Ivanov & Beverton, 1985), 1980s and 1990s (GFCM, 1993) ranked according to their catch value

	Large pelagics	Small pelagics	Demersal
	20%	68%	6%
1960s	*Sarda sarda*—Atlantic Bonito	*Engraulis encrasicolus*—Anchovy	*Scophthalmus rhombus*——Turbot
	Scomber spp.—Mackerel	*Trachurus* spp.—Horse mackerel	*Mullus barbatus*—Red mullet
	Pomatomus saltator—Blue fish	*Sprattus sprattus*—Sprat	*Merlangius m. euxinus*—Whiting
		Alosa pontica—Pontic shad	
	4%	90%	3%
1980s	*Sarda sarda*—Atlantic Bonito	*Engraulis encrasicolus*—Anchovy	*Merlangius m. euxinus*—Whiting
	Pomatomus saltator—Blue fish	*Sprattus sprattus*—Sprat	*Mullus barbatus*—Red mullet
	Scomber spp.—Mackerel	*Trachurus* spp.—Horse mackerel	*Scophthalmus rhombus*—Turbot
		Alosa pontica—Pontic shad	
	1%	79%	7%
1990s	*Pomatomus saltator*—Blue fish	*Engraulis encrasicolus*—Anchovy	*Merlangius m. euxinus*—Whiting
	Sarda sarda—Atlantic Bonito	*Trachurus* spp.—Horse mackerel	*Mullus barbatus*—Red mullet
	Scomber spp—Mackerel	*Sprattus sprattus*—Sprat	*Scophthalmus rhombus*—Turbot
		Alosa pontica—Pontic shad	

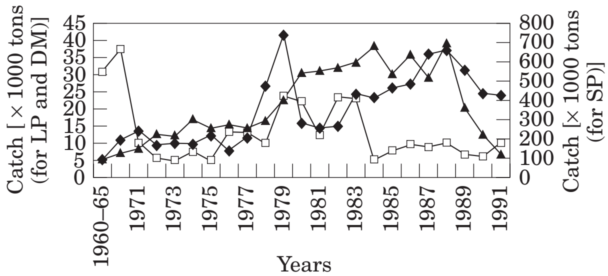

FIGURE 2. Time evolution of the catch of large pelagics (□), small pelagics (▲) and demersals (◆) during the period 1960–1975 (GFCM, 1984).

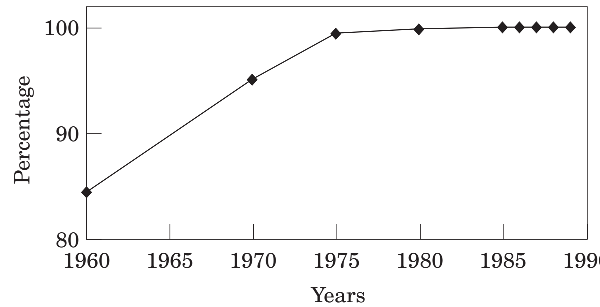

FIGURE 4. Interannual changes in the share of Turkey in the total large pelagic landings (Rass, 1992).

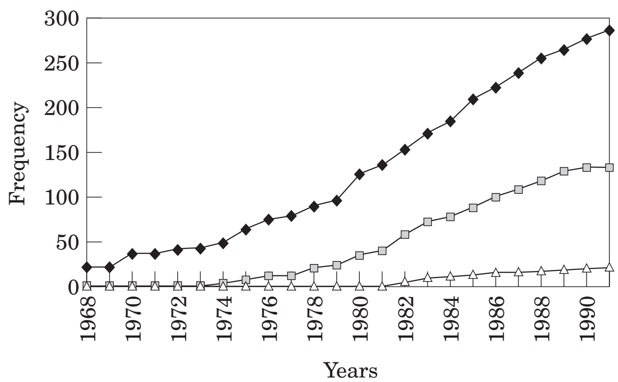

FIGURE 3. Time evolution of the number of Turkish purse seiners (◆), boats with a sonar (□) and boats with a fish pump (△) in the Black Sea (Anon., 1992).

decline in the large pelagics catch was observed (Figure 2). This period coincides with a wide application in the Black Sea of purse seines during the fishing season. Before the 1970s, there were 25 purse seine boats operating along the Turkish coast of the Black Sea (Figure 3). This number doubled in the early 1970s. The target fish of this fishery was the large pelagics of high commercial value. The percentage of the large pelagics harvested from the Black Sea by the Turkish fleet is given in Figure 4, which shows the increase of Turkey's share in the total large pelagics catch. By the end of the 1980s, almost the whole stock was caught during strait crossing and fully exploited. As a consequence, their migration towards the north has been hindered. This period also coincides with the increase of maritime traffic on the Bosphorus (Ozturk & Ozturk, 1996). The destruction of the underwater coastline along the Bosphorus and the increased maritime traffic were also reported to be responsible for the decline in the migratory large pelagics in the Black Sea (Caddy & Griffiths, 1990; Zaitsev, 1993).

The large pelagics, on the other hand, prey upon small pelagics, and as the size of their population was reduced, the controlling mechanism over the small pelagics through predation pressure lessened (Figure 2).

Model results. The mass flow network calculated for the 1960s, when the Black Sea is assumed to have been in a steady-state condition, is depicted in Figure 5. In order to compare the changes in biomass of the ecosystem components calculated for the next two periods with the healthy steady state conditions of 1960s, the biomass of each group in Figure 5 is assigned to unity. As can be seen, the main part of the mass flow takes place between phytoplankton and zooplankton. The phytoplankton production is grazed by the zooplankton and the excess fuels detritus. The gelatinous organisms have not yet reached significant quantities. However, a non-negligible fraction of zooplankton production flows to this group. The small pelagic and demersal fish stocks are not yet overfished. The very low fishery mortality compared to total mortality (Table 6 suggests that these groups were barely exploited). The non-predation natural mortality estimated for the small pelagics is very high for this period. In the model, what is egested (the non-assimilated food) and the part of the group that dies of old age, diseases, etc. (sources of ' other mortality ' or 1-EE) flow to the detritus. A remarkable part of small pelagic production is, therefore, ended in the detritus. This result is quite realistic, as the large pelagics, the main consumer of small eplagics, were at this time under heavy fishing pressure. Another possible explanation for the high natural mortality might be the lack in the ecosystem description of one important group, namely marine mammals, which are not taken into consideration in the present study.

The eutrophication period, 1978–1988

Observations. Towards the end of the 1980s, the changes in the Black Sea ecosystem reached a

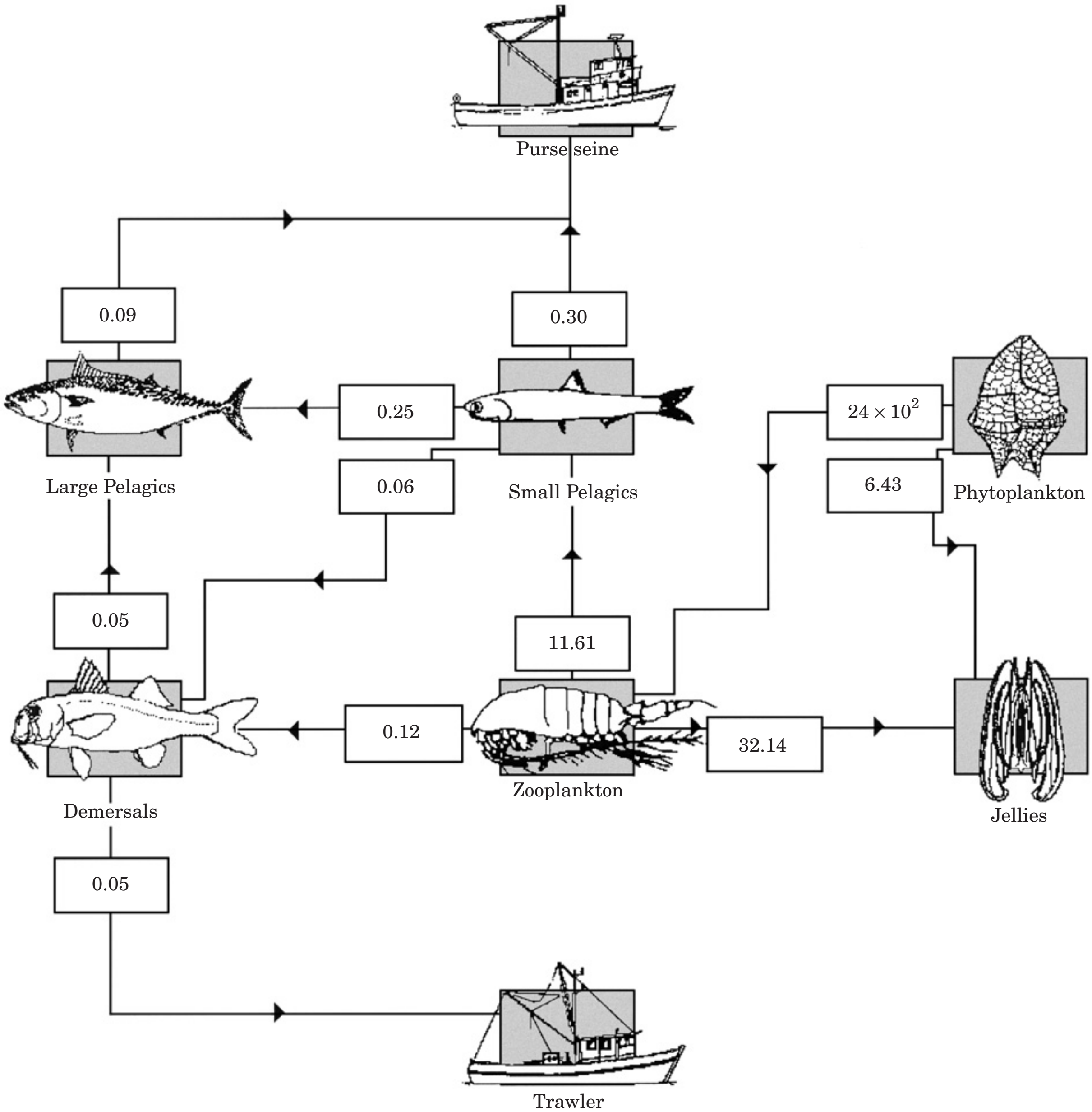

FIGURE 5. Food-web of the Black Sea and the mass transfer between different components during the 1960s. Numbers in the boxes indicate the amount of material transferred in tons km^2 yr^{-1}. The size of the filled boxes represents the biomass of the underwritten group, which are here assigned to unity to enable comparison of the changes taking place at future periods.

dramatic level. For instance, phytoplankton biomass in the north-western shelf area (NWS) had increased by 30 times (Zaitsev & Alexandrov, 1997). Decomposition of the excess production caused hypoxia and even anoxia on the NWS. Within a decade, the surface of hypoxic zones on the NWS increased by one order of magnitude (Zaitsev, 1993). Consequently, the most important spawning ground of the Black Sea fishes of the 1960s deteriorated, and a shift in the spawning ground of fishes towards the south was reported (Niermann *et al.*, 1994).

The absence of predation pressure as a result of the decline of large pelagics stocks, on the one hand, and the eutrophication-related increase of food resources, on the other, created a favourable environment for the small pelagics in the early 1980s (Figure 2). Anchovy was the dominant species within the small pelagics group, and more than 60% of the total catch of Turkey from the Black Sea was due to this short-lived species. The maximum age of the anchovy is 4 years, but the dominant age groups encountered in the catch were age I and II (Ozdamar *et al.*, 1991). However,

Table 6. Model estimates of the annual mortality coefficients for the 1960s data set

Group/coefficient	Z	F	M_0	M_1
Large pelagics	1·70	1·53	0·17	0·00
Small pelagics	2·50	0·23	1·91	0·36
Demersals	2·10	0·56	0·21	1·33

Coefficients (dimensionless): Z=total mortality; F=fisheries mortality; M_0=non-predation natural mortality; M_1=predation mortality.

Table 7. Annual mortality coefficients estimated from the 1980s data set

Group/coefficient	Z	F	M_0	M_1
Large pelagics	1·70	1·53	0·17	0·00
Small pelagics	2·50	1·48	0·25	0·77
Demersals	2·10	1·08	0·21	0·81

Coefficients (dimensionless): Z=total mortality; F=fishery mortality; M_0=non-predation natural mortality; M_1=predation mortality.

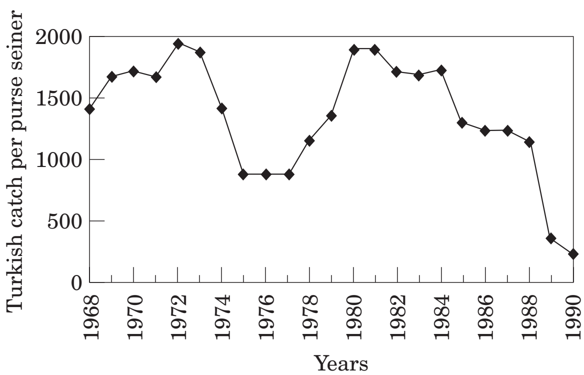

Figure 6. Changes in the Turkish catch (tons) per purse seine boat (Anon, 1992, 1993).

they reach sexual maturity at the end of the first year of their life. The uppermost length distribution given in Figure 8 is the typical length composition of the landing, where the modal lengths correspond to age I and II, and the highest one belongs to age II. This simply implies that the fishing pressure is much higher on the adult individuals, and the spawning stock of the next year is not exploited at a dangerous level. This is a suitable exploitation pattern for the sustainability of the stock. Due to the over-fishing of large pelagics in the 1960s, the purse seines' catch per unit effort dropped sharply (Figure 6), and their interest diverted to small pelagics. The catch per purse seine of the fleet reached a second maxima in 1980 (Figure 6). Again, the fishery became a profitable sector and called the attention of investors. While the number of boats were increasing, the existing boats were equipped with powerful sonar, fish pumps and auxiliary skiffs, which increased the fishing power of the fleet (Figure 3; Anon., 1992). In the mid-1980s, the total catch of the Turkish Black Sea fishing fleet exceeded the demand of the consumer market and the unit price dropped drastically (Anon., 1993). However, in order to utilize the increased fish resources, the Turkish Government encouraged fish processing factories through low interest loans and induced the uncontrolled growth of such factories. Today, the fishing and processing capacities of Turkey are not properly matched, i.e. the total capacity of fish processing factories is 6700 tons day^{-1}, which is 4 times higher than the total annual production of the whole country, including catches from the Mediterranean, Aegean, Marmara and inland waters (Gucu, 1997).

The enhanced phytoplankton growth did not only stimulate small pelagics. Other zooplanktivorous groups, such as *A. aurita*, reached very high biomass values (400 million tons; Gomoiu, 1981).

Model results. For the 1980 period, the model is constrained by the recorded biomass of phytoplankton (Nesterova, 1987) and gelatinous organisms (Gomoiu, 1981). The high phytoplankton biomass value reflects the increased eutrophication during this period (Figure 7). The biomass of gelatinous organisms is entered as 952 tons km^{-2}. This value reflects the pre-*Mnemiopsis* period, during which there were only *A. aurita* in the ecosystem. The model predicts a shrinking large pelagics group and a considerable increase in the small pelagics and demersals as an indirect consequence of increased phytoplankton growth. The zooplankton biomass needed to sustain the gelatinous organisms and the small pelagics was calculated as 660 tons km^{-2}. This value is 20 times higher than the zooplankton biomass estimated for the 1960–1965 period (Ivanov & Beverton, 1985). Despite the excessive increase in the zooplankton biomass, the ecotrophic efficiency of the phytoplankton group was estimated as 0·45, indicating that about 50% of the phytoplankton production fuelled the food-web, while the rest was accumulated as detritus. This huge phytoplankton-derived detritus is a sign of increasing eutrophication.

The total mortality coefficient of the fish groups remained unchanged, since P/B ratios were kept constant in all model runs. However, the mortality changed remarkably (Table 7). The fishery mortality

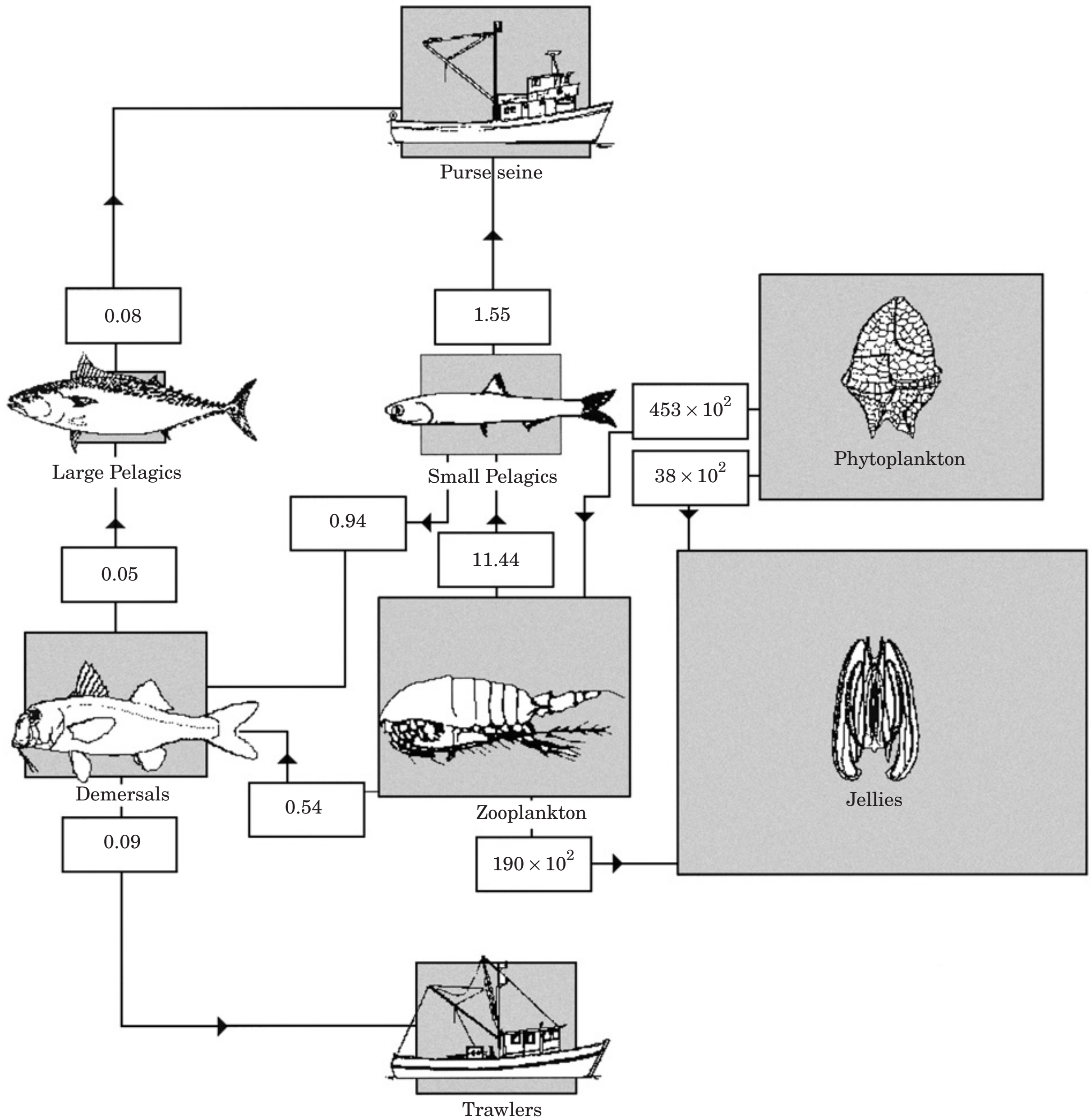

FIGURE 7. Food-web of the Black Sea and the mass transfer between different components during the 1980s. The size of the filled boxes represent the biomass of the group normalized to the biomass of the same group in 1960s. The numbers in the shaded rectangles indicate the amount of material transferred in tons km^2 yr^{-1}.

coefficient of small pelagics increased due to the increased fisheries pressure. During this period, almost 60% of the total mortality was attributable to the fisheries. The increase in the exploitation rate is evident from the decrease in the other mortality coefficient, M_0.

The period of ' collapse and recovery ', 1988–1995

Observations. The first signs of overfishing on the small pelagic group were realized during the 1987–1988 fishing season. The total landing of the Turkish fleet during the 1987/1988 and the 1988/1989 fishing seasons was almost the same, but the size of the fish caught in 1988/1989 was remarkably lower. This indicates that the anchovy stock had already exceeded a sustainable level in 1987/1988. In order to reach the same catch level, the fleet caught mainly newly recruited, small-sized fishes in 1988/1989 (Figure 8). Consequently, the stock collapsed the year after. Since the giant fishing fleet and the processing factories were in endless demand for fish, the fleet also depleted the

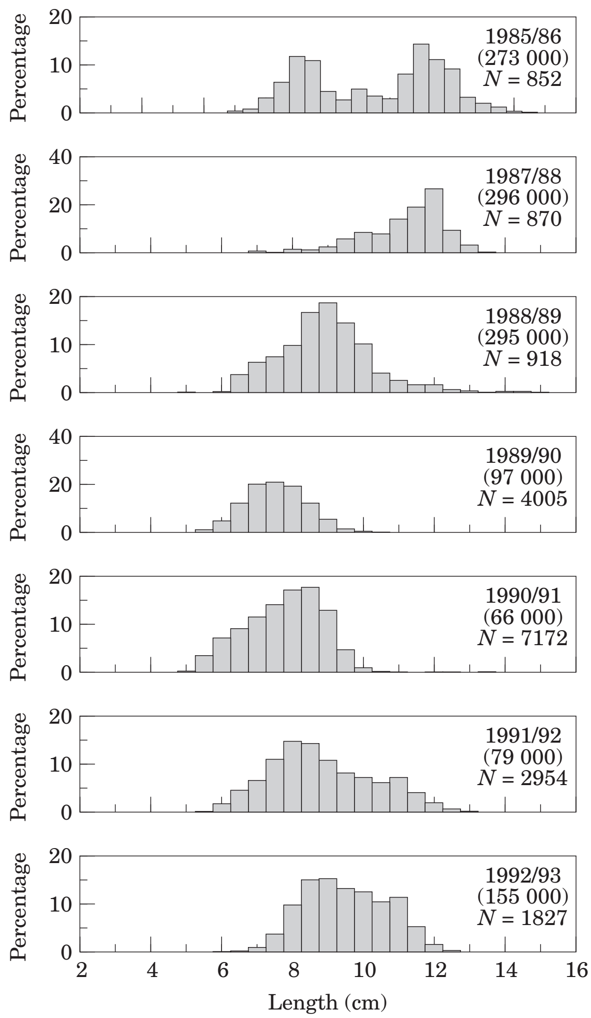

FIGURE 8. Time series of the length composition of anchovy landed by the Turkish Black Sea fishing fleet (data from Ozdamar *et al.*, 1991 & Bingel *et al.*, 1993).

juveniles without any concern for marketing. As a result, in 1989/1990, the total anchovy catch of Turkey was only 90 000 tons (Anon, 1993). Moreover, the catch included subadult anchovies, which had not yet attained sexual maturity. This indicates that the Black Sea anchovy faced a recruitment failure. Indeed, the size of the spawning stocks was reduced to such an extent that they could not produce enough offspring to sustain future generations.

The analysis of the gonadosomatic indices of the anchovies before and after the collapse of the fisheries industry (Gucu, 1997) suggested that the newly recruited anchovies at the period of the fisheries crisis (1989/1990) were in better condition compared to before the crisis. This is hardly surprising, because as the size of the anchovy stock depleted, food availability to the juvenile anchovies, as well as other planktivorous organisms, increased.

This period also corresponded to the introduction of *M. leidyi*. Vinogradov *et al.* (1989) reported 840 000 tons of *M. leidyi* for the entire Black Sea. This is, in fact, not an extreme biomass for the Black Sea, because even well before this period, gelatinous carnivorous *A. aurita* had already reached such high biomass in the Black Sea (Figure 1). *Aurelia aurita* is a Cnidarian and its life-cycle involves an asexually reproducing polyp stage, which requires a substrate to settle (Brusca, 1990). Reproduction is, therefore, restricted to coastal waters, where the availability of a substrate within the oxygenated zone is incomparable. In contrast, the Ctenophore, *M. leidyi* sheds the gametes directly into the surrounding seawater where fertilization takes place (Brusca, 1990). This reproduction mode presumably gave *M. leidyi* an advantageous position in the medium-level trophic level interspecies competition in the Black Sea. Consequently, at the period of high *M. leidyi* biomass, a sharp decline in *A. aurita* was reported.

Model results. The above changes in the ecosystem are reproduced by the model of flow network (Figure 9). As in the previous calculation, the model is constrained by the gelatinous (Mutlu *et al.*, 1994) and phytoplankton biomass (Nesterova, 1987). In this experiment, the gelatinous organisms consist of all three species listed in Table 1. Their overall biomass is noticeably low compared to the previous period. The calculated biomass of small pelagics is accordingly low. The minimum zooplankton biomass needed to supply planktivorous organisms in the system is calculated by the model as 148 tons km^{-2}, which is only four times higher than in 1960–1965 period (Figure 5). When compared to the 1980s period, much less zooplankton is needed to support the ecosystem. This implies that if the field observations of phytoplankton and gelatinous organisms used in the model represent the real situation in the Black Sea, there is no doubt that there was enough food for the small pelagics at the time of the fisheries collapse (1989–1990).

As a consequence of overfishing, the fish compartments were remarkably reduced. The induced phytoplankton production flowing through the phytoplankton→zooplankton→fish pathway, and modifying the carrying capacity of the small pelagics at the beginning of the 1980s, was blocked by heavy fishing pressure during this period. The flow of excess biological material is diverted, to a great extent, in favour of gelatinous organisms and hence benefits first, *A. aurita* in the 1980s, and later, *M. leidyi* in the 1990s. As already shown in Table 4, the gelatinous organisms are all trophic dead-ends. The mechanisms

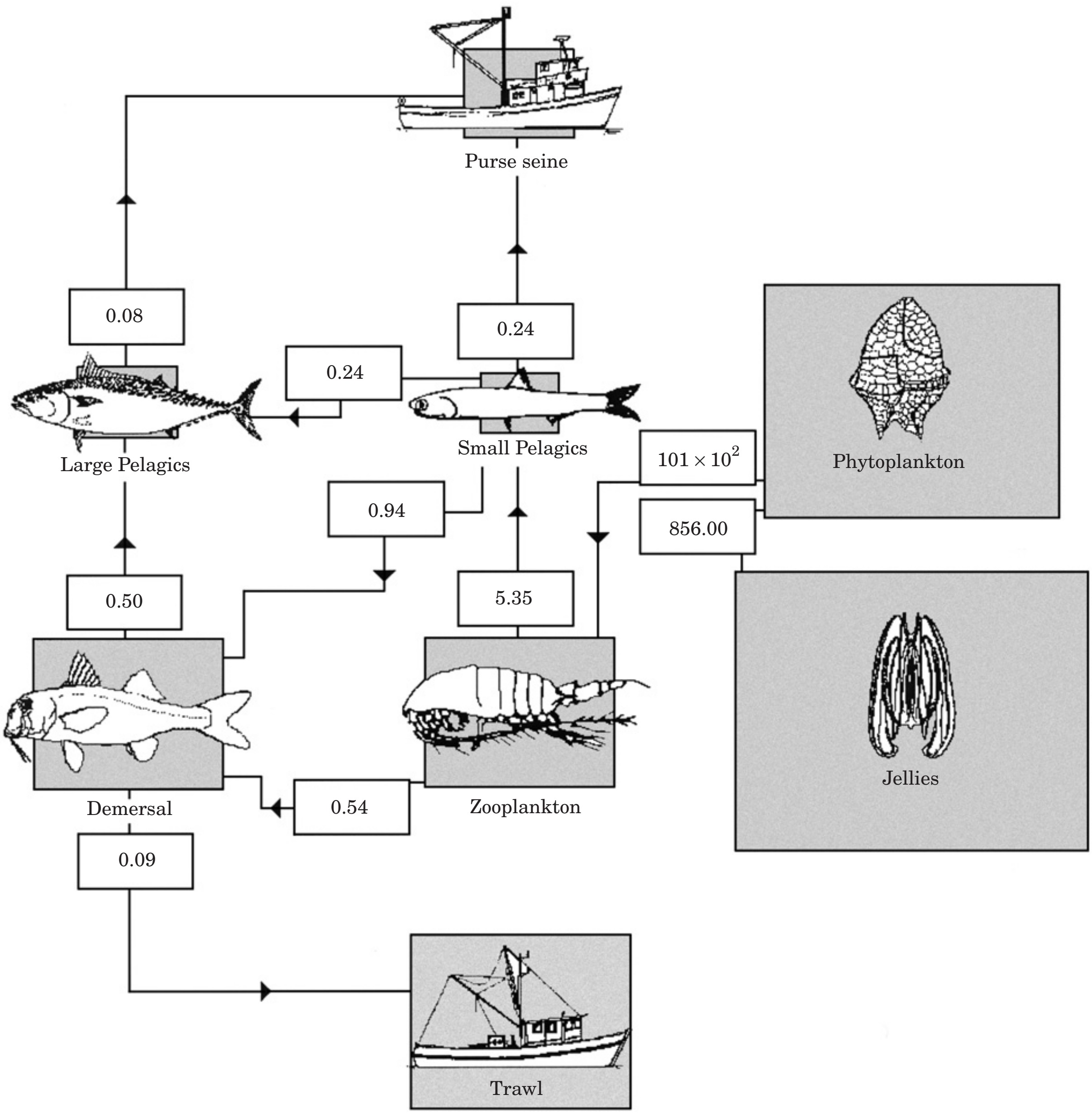

FIGURE 9. Food-web of the Black Sea and the mass transfer between different components during the 1990s. The size of the filled boxes indicates the changes in the biomass with regard to the 1960s. The numbers in the shaded rectangles indicate the amount of material transferred in tons km^2 yr^{-1}.

controlling the population size of this group are food availability and natural mortality. The size of the gelatinous populations in the Black Sea can only be controlled by the competing groups occupying the same trophic level and competing for the same food source, which is essentially the small pelagics. To reverse the situation in the Black Sea, model results indicate that the fisheries pressure on the small pelagics should be removed by reducing the existing extreme fishing effort. As a matter of fact, the catch per effort and, in turn, total income of the fishermen has been reduced as a result of the drastic decline in stocks. Faced with declining anchovy catches, the Turkish fishing fleet of the Black Sea, which had attained enormous proportions, correspondingly shrunk slightly. Some of the fishermen switched to alternative businesses, while others moved to the Aegean and Mediterranean Seas to cope with the crisis. The Turkish Government finally decided to stop further development of the fishing fleet along the Turkish coast in 1993. According to the latest catch statistics, the Turkish fisheries are now experiencing a slight recovery. With further attempts to reduce the size of the fishing effort on the Black Sea, fish stocks can be recovered.

Conclusion

The combined analysis of ecological observations, fisheries data and mass balance model experiments indicate that overfishing did play a crucial role in the successful development of *M. leidyi*, by emptying the ecological niche occupied by small pelagic fishes and allowing gelatinous competitors to re-inhabit. The recovery of the ecosystem relies, to some extent, on management attempts to level-out fisheries at a sustainable level.

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