MODELING TROPHIC INTERRELATIONSHIPS IN THE BLACK SEA

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Abstract. The Black Sea being one of the largest enclosed seas, has been subjected to severe ecological changes within the last few decades. The river induced nutrient enrichment and eutrophication caused significant changes in the species composition. Some of species have disappeared while some others were newly introduced and became dominant in the Black Sea ecosystem. Among those which dominated the pelagic ecosystem, gelatinous organisms suddenly attained a high level of biomass in 1989, which can hardly be supported by the existing trophodynamic structure.

Four balanced steady state models, corresponding to 1960's, before and after outburst of the gelatinous organism and the present state of the ecosystem, are used to illustrated the changes in biomass and food consumption among major ecological groups of the Black Sea. The model considers trophic interactions among the six compartments of the ecosystem involving phytoplankton, macrozooplankton, gelatinous carnivores, demersal fishes, small and large pelagics. The results demonstrated gaps in our knowledge on food web structure and on the productivity of the important groups.

1. Introduction

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

Distinguishing signatures of the ecosystem changes are the domination of some species especially those adopted to eutrophic conditions and a decrease in biodiversity (Zaitsev, 1992). The most striking example is the gelatinous animals; the biomass of *Aurelia aurata* has increased with increasing eutrophication of the Black Sea (Caddy and Griffiths, 1990). From 1950-62, Shushkina and Musayeva (1983) found a biomass in the order of 30 million tons wet weight. In 1978 a much larger biomass, as large as 400 million tons wet weight for the whole of the Black Sea was calculated by Gomoiu (1981). Almost same figure was given by Flint et al. (1989).

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Finally, in 1989 *Mnemiopsis sp.*, which is an 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 Mnemiopsis 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 author focused on possible predation of *Mnemiopsis sp.* on anchovy egg and larvae and sought correspondence with collapse of anchovy fishery (Vinogradov, 1990; Zaika, 1992; Harbison and Volovik, in press). On the other hand, neither carrying capacity (even though raised up significantly by the continues nutrient pump through the rivers), nor the trophodynamic structure of the Black Sea do not support such a high biomass value of *Mnemiopsis sp.* reported in 1989.

The purpose of this study is to model the changes in the Black Sea ecosystem for different ecological periods. It is also aimed to reveal impact of ever increasing phytoplankton productivity and the fishery on the ecosystem. Finally, by taking trophodynamic interactions among its different components and carrying capacity, maximum biomass level of jelly organisms that can be found in the Black Sea is questioned.

2. Material and Method

To estimate mass flow among different ecosystem components ECOPATH model has been used (Cristensen and Pauly, 1992). The model assumes the following steady-state balance equation.

Production by (i) - predation on (i) - non predation losses of (i) - export of (i) = 0

$$B_i * PB_i * EE_i - \sum_{j=1} B_j * QB_j * DC_{ji} - EX_i = 0 \quad \ldots\ldots\ldots\ldots 1$$

where: B_i is the biomass of i,

PB_i is the production/biomass ratio of i,

EE_i is the Ecotrophic Efficiency of (i),

QB is the consumption/biomass ratio,

DC_{ji} is the fraction of prey (i) in the average diet of predator j.

EX_i is the Export of (i)

Based on this equation, for a system with n groups, n linear equations can be given

$$B_1.PB_1.EE_1 - B_1.QB_1.DC_{11} - B_2.QB_2.DC_{21} - \ldots - B_n.QB_n.DC_{n1} - EX_1 = 0$$
$$B_2.PB_2.EE_2 - B_1.QB_1.DC_{12} - B_2.QB_2.DC_{22} - \ldots - B_n.QB_n.DC_{n2} - EX_2 = 0$$

:

:

$$B_n.PB_n.EE_n - B_1.QB_1.DC_{1n} - B_2.QB_2.DC_{2n} - \ldots - B_n.QB_n.DC_{nn} - EX_n = 0$$

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

$$[A]_{n,m} * [X]_m = [Q]_m$$

with n being the number of equations, and m the number of unknowns.
Given the inverse A^{-1} of the matrix A, this provides

$$[X]_m = [A^{-1}]_{n,m} * [Q]_m$$

For the simplicity of calculation the Black Sea Ecosystem is defined by 7 components. Major species grouped under these components are given in Table 1.

TABLE 1. Ecosystem components used in the model and the major contributes

Pelagics *Pomatomus saltatrix* *Sarda sarda* *Scomber japonicus* *Scomber scombrus*	**Demersals** *Merlangius merlangus euxinus* *Mullus barbatus poticus*
Small Pelagics *Alosa spp.* *Engraulis encrasicolus* *Clupeonella cultriventris* *Sprattus sprattus* *Trachurus mediterraneus*	**Jellies** *Aurelia aurata* *Mnemiopsis sp.* *Pleurobrachia pileus*
Zooplankton Microzooplankton	**Phytoplankton** Net phytoplankton
Harvesters Purse seiners Trawlers	

The Ecopath model is a steady state model and since state of today's Black Sea Ecosystem is unbalanced by the factors discussed above, the data from most recent period (1960's) when the Black Sea was believed to be in steady state condition was used to initialize the model (Table 2a). It is assumed that intrinsic parameters, such as the production/biomass ratio, consumption/biomass ratio, do not differ much with the changes taking place in the Black Sea and using same parameters estimated for steady state period, two trials have been made for two different jelly-fish biomass estimates (Table 2b).

TABLE 2a. Input data for 1960's. The parameters P/B, Q/B and EE are as described in eq.1

Group	Biomass (10e3 t)	Production (10e6 t)	P/B	Q/B	EE	Harvest (10e3 t)
Large Pelagic	300[1]		1.7	8.7[6]		37.4[4]
Small Pelagic	5 000[1]		3.0[11]	7.9[6]		125.0[4]
Demersal		0.09[1]	2.1	12.0[6]	0.95[8]	19.8[4]
Jellies	675[3]		10.0[7]	39.2[7]		
Zooplankton	15 600[2]		67.0	137.0[5]		
Phytoplankton	3 700[1]	1 213.60[1]	328.0			

Interrelations between different ecosystem components were described by a prey/predator matrix shown at Table 3. Migratory components such as Large Pelagics like *Sarda sarda, Pomatomus saltatrix* and Small Pelagics, such as *Trachurus mediterraneus* migrates to southern seas. Therefore taking the time period spent outside the Black Sea into account, it is assumed that a portion of their food requirement were fulfilled by an external source and hence an import term is added to the matrix.

TABLE 2b. Input data for 1980's and 1990's

Group	Biomass (10e3 t)	P/B	Q/B	EE	Harvest (10e3 t)
Large Pelagic	50	1.7	8.7[6]		35[4]
Small Pelagic		3.0	7.9[6]	0.90[8]	652[4]
Demersal	175[9]	2.1	12.0[6]		37[4]
Jellies (1980's) (1990's)	400 000[10] 100 000[12]	10[7]	39.2[7]		
Zooplankton		67	137.0[5]	0.90[8]	
Phytoplankton	100 000[11]	328			

Data have been taken from

1) Greze, 1979; 2) Ivanov & Beverton, 1985; 3) Mironov 1971;
4) GFCM, 1993; 5) Petipa, et al., 1973; 6) Palomares & Pauly, 1989;
7) For the present analysis a gross food conversion efficiency of 0.25 is assumed and the Q/B is calculated from the P/B ratio using this efficiency
8) Estimated based on an assumed Ecotrophic efficiency of 0.9 for the group, i.e. 90% of the fish production is used in the system for predation or for catch.
9) Intuitively calculated using catch values and recent biomass estimates of Bingel et al., 1993
10) Gomoiu, 1981 11) Nesterova, 1987 12) $Z \approx P/B$ (Allen, 1971)
13) Mutlu et al. (1994)

TABLE 3. Food matrix used in the model

Prey \ Predator	L. Pelagic	S. Pelagic	Demersal	Jellies	Zooplankton
L. Pelagic	0	0	0	0	0
S.Pelagic	0.30	0	0.50	0	0
Demersal	0.20	0.02	0.20	0	0
Jellies	0	0	0	0	0
Zooplankton	0	0.85	0.30	0.50	0.20
Phytoplankton	0	0.08	0	0.10	0.50
Detritus	0	0	0	0.40	0.30
Import	0.50	0.05	0	0	0
Sum	1	1	1	1	1

Data used to compile food matrix:

Avsar, 1994
Ismen, 1994
Slastanenko, 1956
Tsikhon-Lukanina and Reznichenko, 1991

Reliability of the model outputs and consistency of the results were analyzed by the following ecological terms:

Respiration is calculated as the difference between the assimilated part of the consumption and the part of the production that is not attributed to primary production, since the assimilated food ends up as either production or respiration. The respiration should therefore be a non-negative value.

The part of the food intake that is assimilated is computed for each consumer group from

$$B_i * QB_j * (1-GS_i)$$

where: B_i is the biomass of group i,
QB_i is the consumption/biomass ratio of group i,
GS_i is the part of the consumption that is not assimilated and here assumed as 20% for all groups included.

GE, the gross food conversion efficiency; is the ratio between production and consumption. In normal cases, the GE will be in the range of 0.1 to 0.4 as the consumption of most groups is about 3-10 times higher than their production.

Production/Respiration; production to respiration ratio can take any positive value, though thermodynamic constraints limit the realized range of this ratio to values lower than 1 (Christensen and Pauly, 1992).

Sensitivity of the model is tested using Leontif's (1951, cited in Christensen and Pauly, 1992) matrix, which shows the impact of the increase of biomass at time t in a group row can cause on the others (columns) at time t+1. This matrix also allowed to assess the direct and indirect interactions in the Black Sea ecosystem.

The simulated changes in the ecosystem are depicted in box charts in which the size of the boxes at steady state figure are assigned to unity and the changes took place at later periods were represented by the changes in the size of the boxes .

3. Results

Initially the model was deployed for four different stages of the Black Sea Ecosystem; steady-state phase, just before Mnemiopsis outburst (1980's), Mnemiopsis case (1989) and more recent stage (1990's). In the following, results obtained only for the 3 different states were given, because the Mnemiopsis estimates given in the literature for the year 1989 were so high that, it was not possible to balance flows between components.

The output of the model deployed for steady-state period (1960's) is given Table 4a. The only missing parameters computed by the model is the biomass of "Demersals" and it was calculated as 1 650 000 tons. The Ecotrophic efficiencies (**EE**), food conversion efficiency (**GE**) and production/respiration ratio for each group were also presented at Table 4a. Keeping component specific rates unchanged, and assigning zooplankton biomass as unknown, model has been deployed for pre- and post Mnemiopsis phase of the Black Sea Ecosystem. The outputs were given in Table 4b and 4c.

TABLE 4a. Model output for steady state period. The framed numbers are the estimates computed by the model. Biomass values and harvest are in thousand tons, the others are unitless.

Group Name	Biomass	P/B	Q/B	EE	GE	P/R	Harvest
Large Pelagics	300	1.7	8.7	0.000	0.20	0.195	37.4
Small Pelagics	5000	3.0	7.9	0.712	0.38	0.521	125.0
Demersals	1650	2.1	12.0	0.950	0.18	0.210	19.8
Jellies	675	10.0	39.2	0.000	0.25	0.250	-
Zooplankton	15000	67.0	137.0	0.967	0.23	0.302	-
Phytoplankton	3700	328.0	0.0	0.859	-	-	-

How the different components of the ecosystem has changed in quantity as compared to steady state phase, were shown in Figure 1a - 1c. Some groups like all kinds of fishes were decreased whereas Phytoplankton, Zooplankton and Jellies biomass raised to enormous quantities.

TABLE 4b. Model output for *pre-Mnemiopsis* period (Data for jelly-fish biomass was taken from Gomoiu, 1981). Biomass values and harvest are in thousand tons, the others are unitless.

Group Name	Biomass	P/B	Q/B	EE	GE	P/R	Harvest
Large Pelagics	50	1.7	8.7	0.000	0.20	0.195	35.0
Small Pelagics	437	3.0	7.9	0.900	0.38	0.577	652.0
Demersals	175	2.1	12.0	0.996	0.18	0.212	37.0
Jellies	400,000	10.0	39.2	0.000	0.25	0.250	-
Zooplankton	243,268	67.0	137.0	0.900	0.49	0.874	-
Phytoplankton	100,000	328.0	0.0	0.562	-	-	-

TABLE 4c. Model output for *post-Mnemiopsis* period (Data for jelly-fish biomass was taken from Mutlu et al., 1994). Biomass values and harvest are in thousand tons, the others are unitless.

Group Name	Biomass	P/B	Q/B	EE	GE	P/R	Harvest
Large Pelagics	50	1.7	8.7	0.000	0.20	0.195	21
Small Pelagics	437	3.0	7.9	0.900	0.38	0.577	374
Demersals	175	2.1	12.0	0.996	0.18	0.212	28
Jellies	100,000	10.0	40.0	0.000	0.25	0.250	-
Zooplankton	60,897	67.0	137.0	0.900	0.49	0.874	-
Phytoplankton	100,000	328.0	0.0	0.141	-	-	-

No real difference in Leontif's matrix was observed between 1980's and 1990's, therefore they are represented by the same figure (Figure 2b). Since the food requirement and the food preference matrix of the ecosystem components were kept constant in all periods examined, impacted/impacting pattern has not changed in shape

but the magnitude of the impacts were altered (Figure 2,a,b). In general, these figures reflect direct relations between groups, i.e. predators have always negative impact on preys. The competitions between groups located at the similar trophic levels are also well presented in these figures.

In 1960's the key component or in other words the most sensitive group of the ecosystem is the zooplankton. The largest impacts are observed on the zooplankton group. The group "Jellies" has nearly no effect on the other components of the Black Sea ecosystem in 1960's. However later in 1980' and 1990's their impact on other groups are evident and mostly negative.

The consequences of the over-fishing is clearly seen from the figures. As small pelagics increase, the fishery increases in both periods. But in turn, when the fishery is increased, large pelagics diminish drastically.

In Table 5. summary of the system is given, where total production in the Black Sea has increased nearly 20 times; total calculated primary production is 26 times higher in 1990's as compared to 1960's; total biomass in the Black Sea in 1990's is 10 times higher than 1960's while total consumption is increased only 5 times.

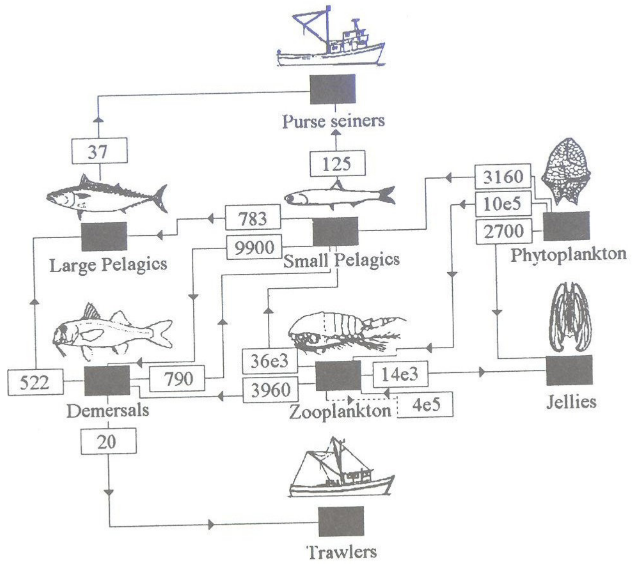

Figure 1a. Food web of the Black Sea and the flows between different components in 1960's. The size of the boxes is kept equal to enable comparison of the changes taken place at the future periods.

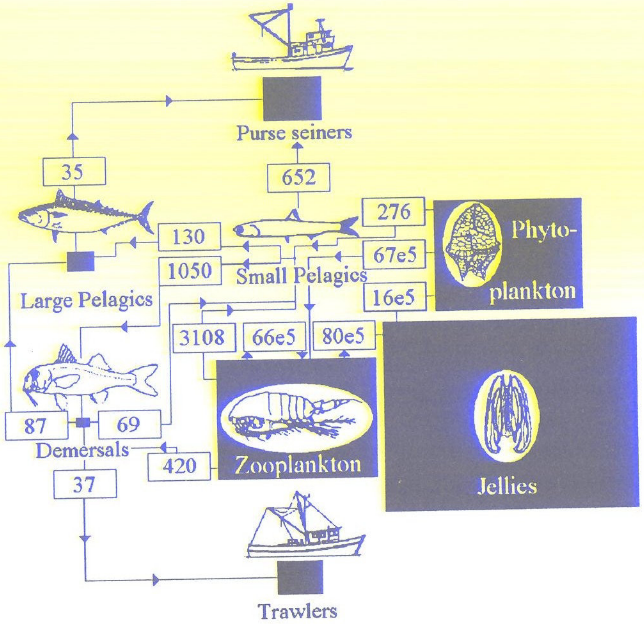

Figure 1b. Food web of the Black Sea and the flows between different components in 1980's. The size of the boxes is kept equal to enable comparison of the changes taken place at the future periods.

4. Discussion

The reliability of the data, which were taken from literature to simulate steady state case of the Black sea ecosystem (Table 1a and Figure 1a) were tested by the accuracy of EE, GE and P/R values. The results were all ranged within their limits, so that the outputs were considered appropriate for further evaluation. The Leontif's matrix drawn for this period (Figure 2a) showed that the most crucial component of the ecosystem is the zooplankton, which is in fact major limiting food source of such an ecosystem. For 1980's and 1990's the zooplankton biomass compartment of the model left unknown. By taking the food requirement of all components in the account the model estimated a biomass value. For 1980's when total biomass of *Aurelia aurata* is reported as 400 million tons, the estimated zooplankton standing biomass is calculated as about 250 million tons, which is almost 15 times higher than the steady state conditions. In general, an increase in the secondary production is an expected consequence in a developing system where total production is enhanced by extreme extraneous nutrient input, however the value obtained by the model is far beyond acceptable range.

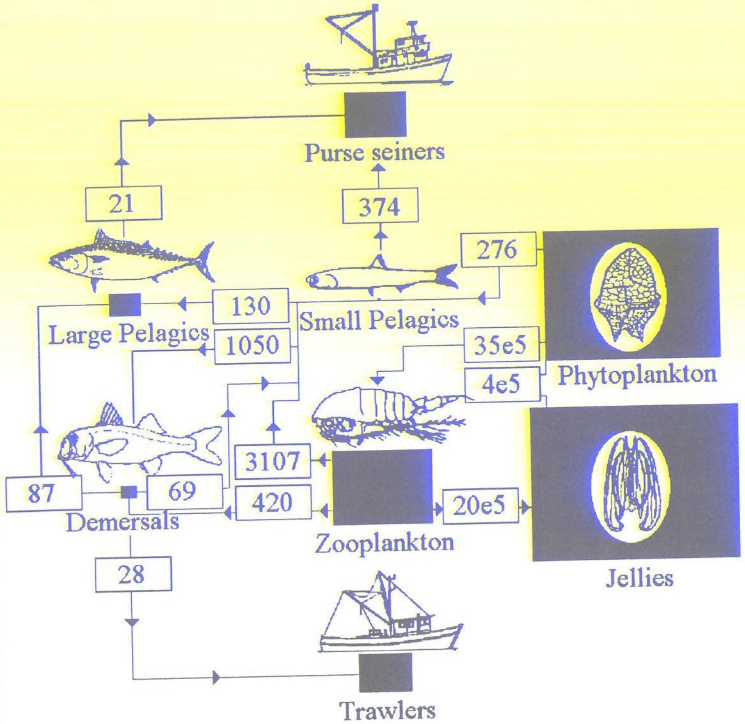

Figure 1c. Food web of the Black Sea and the flows between different components in 1990's. The size of the boxes is kept equal to enable comparison of the changes taken place at the future periods.

TABLE 5. Summary statistics of the net flow for the model. Biomass are given in tons.

Statistics	1960's	1980's	1990's
Σ consumption (X e6)	2.144	49.333	11.057
Σ system throughput (Xe6)	3.809	83.997	18.698
Σ all production (X e6)	1.708	52.801	36.950
Σ calc.net PP. (X e6)	1.203	32.500	32.500
Net system production (X e6)	0.463	2.163	24.858
Σ biomass	26 325	743 930	252 126

In 1990's case, the data for the total biomass of jelly organisms are taken from Mutlu et.al (1994). The model results are fairly consistent with the expectations. Zooplankton standing biomass is only 4 times higher than the that of 1960's value (Table 4c). The EE value for the phytoplankton is now only 0.121 which is low enough to be acceptable for Black Sea ecosystem as far as recent ecological state of the Black Sea concerned, which shifts from oligotrophy to eutrophy is concerned (Odum, 1969).

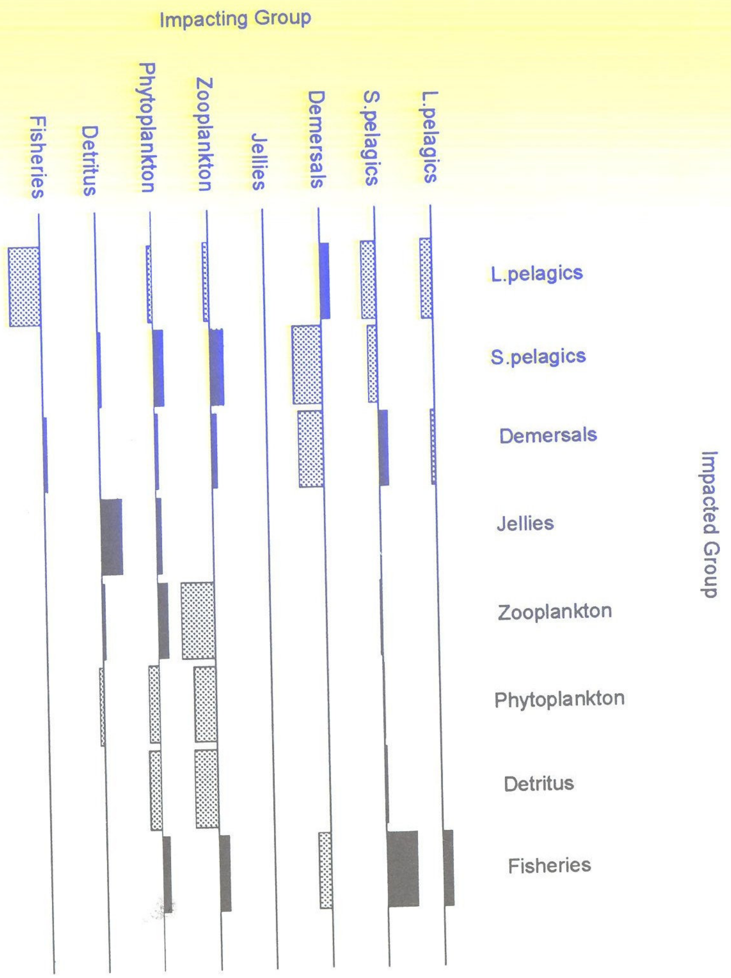

Figure 2.a Mixed trophic impacts in Black Sea ecosystem during 1960's. Negative impacts are indicated by shaded bars pointing left, while the black bars pointing right show positive impacts.

Another important finding resulted from the model is the inconsistency in the ratio between total system biomass and the total consumption. In 1990's this ratio is nearly the half of the value calculated for 1960's, which is an evidence of food shortage in the ecosystem in general.

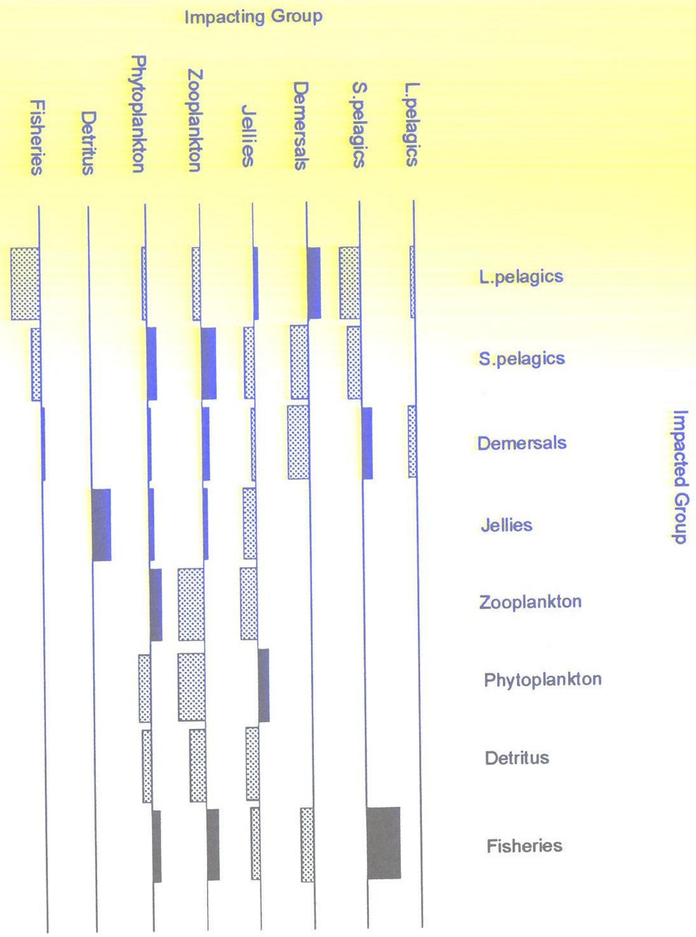

Figure 2.b Mixed trophic impacts in Black Sea ecosystem during 1990's. Negative impacts are indicated by shaded bars pointing left, while the black bars pointing right show positive impacts.

5. Conclusion.

The major finding of the study is the biomass estimates given for the *Mnemiopsis* at the outburst periods and the biomass of the *Aurelia aurata* are unacceptably high as far as their food requirement is concerned. Simply, assuming that zooplankton is the major food source for the jelly organisms there is not enough food to sustain for such a high biomass value given in the literature. The most probable explanation to this situation is; i) either because of clumped distribution of the jelly organisms, and due to limited number of samples, the estimated mean biomass values are not representative enough to extrapolate to whole basin or ii) there is another trophic component in the ecosystem, which has been overlooked so far and which meets significant portion of the food requirement of gelatinous organisms. In both cases, there is very little fear of negative impacts of jelly organisms on fish stocks, who stand at the same trophic level.

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