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INFLUENCE OF GELATINOUS ZOOPLANKTON ON FISH STOCKS IN THE BLACK SEA: ANALYSIS OF BIOLOGICAL TIME-SERIES

Scientific information about the Black Sea ecosystem with respect to jelly plankton – fisheries interactions is reviewed. Long time-series of the main components of pelagic community: fishes, invertebrates, discussed trends, and relationships between them are analysed. The amount of information and results from the analyses will be used to formulate hypotheses about the linkages between gelatinous plankton and the other pelagic populations and the effects on fish stocks. These data will be used as a background study for the following stages in the Eurogel project: experimental work, data analyses and modelling.

Key words: jellyfish, *Mnemiopsis leidyi*, zooplankton, anchovy, sprat, horse mackerel, *Beroe ovata*, introduction, time-series, Black Sea

Human-induced factors such as eutrophication, heavy fishing, and the introduction of exotic species have been evoked to explain the Black Sea ecosystem changes in recent decades [4, 32, 54]. Natural abiotic and biotic factors responsible for the basic physical, chemical and biological processes in the sea were also explored aiming to provide explanations of the ecosystem dynamics [11, 12, 29, 31].

By the early 1970s, pelagic top-predators (dolphins, bonito, and bluefish) were greatly reduced [11]. Subsequently, the stocks of small pelagic fishes increased considerably and became a target for the industrial fishery. In the mid 1980s, the total catch approached one million tones, about 65 % of which was anchovy and about 20 % sprat and horse mackerel [32]. The jellyfish *Aurelia aurita* (L., 1758) became dominant in the early 1980s [41]. By the late 1980s, *A. aurita* was replaced in terms of dominance by the exotic ctenophore *Mnemiopsis leidyi* (Agassiz) [42]. Meanwhile, zooplankton biomass decreased almost twofold compared with the 1960s, and phytoplankton standing crop doubled [45, 46] during the 1980s. The frequent phyto- and gelatinous plankton blooms and the bulk of unutilised biomass produced a shift in the water quality to a state characterised by low transparency and high production of detritus, causing oxygen depletion and hypoxia near the bottom [54, 55]. Increased mortality of mussels and other benthic filter feeders [35, 14, 15] contributed to the increase of unutilised detritus, oxygen depletion and hydrogen sulphide production on the shelf.

During the period of observation (1960 – 2001), the Black Sea pelagic ecosystem went through some major transformations. According to several indicators of ecosystem health (species diversity, nutrient conservation, production, and utilisation of detritus, trophic efficiency) since the 1960s the Black Sea ecosystem degraded to a less stable and immature (sense E. P. Odum) state [3, 9, 23]. This state was characterised by dominance of fewer and smaller opportunist species with short life cycles and quicker turnover rates. Production of organic matter and detritus heavily dominated predation and recycling and ecosystem control mechanisms were seriously disturbed. These instable conditions favoured the introduction and outburst of *M. leidyi.* Gelatinous zooplankton is known to be highly opportunistic and *M. leidyi* as the jellyfish *A. aurita* during the 1980s took advantage from the deteriorated conditions and the increased productivity. By the late 1990s, the *M. leidyi* population stabilised and reinforced the predatory control on the prey zooplankton biomass.

The introduction and outburst of *M. leidyi* was accompanied by reduction in abundance of the almost all components of the plankton community since 1988 and affected the stocks of some abundant commercial fish species. *M. leidyi* invasion has been associated with the fisheries collapse during the early 1990s and it is very important to evaluate the damage caused by *M. leidyi* on commercial fish populations. The key problem here is to reveal the preconditions of penetration of exotic species and formation of their highly productive populations in the Black Sea.

Materials and methods. Analysis covered the material collected by the Institute of Fisheries and Aquaculture, Varna and the Southern Scientific Research Institute of Marine Fisheries & Oceanography (YugNIRO), Kerch for the period 1960 – 2003. Sampling was conducted in all seasons during the year. Besides the standard network of the complex oceanographic stations (Fig. 1) samples were occasionally collected in some other areas in the center of the sea and along the coasts of Romania, Bulgaria and Turkey.

At each station and for several depth strata standard oceanographic parameters (temperature, salinity, and oxygen content) were measured. Phytoplankton was sampled using bathometers. Jaddy's net with diameter 37 cm and Bogorov-Rass' net with the diameter 80 cm were used to sample mesozooplankton.

During 1965 – 1988, jellyfish *A. aurita* was sampled using 23-meter pelagic trawl with opening of 5 m designed by N. N. Danilevsky [7]. Trawlings were made according to the standard network of the stations. The trawling duration was 30 minutes by circulation at the vessel's

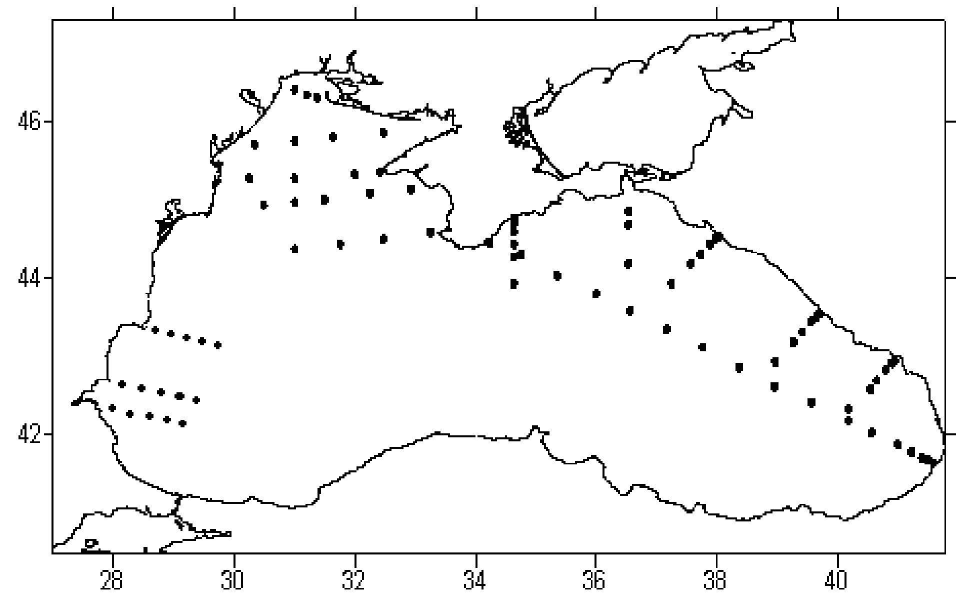

Fig. 1 Scheme of complex oceanographic stations in the Black Sea

Рис. 1 Схема комплексных океано-графических станций в Чёрном море speed of 2.5 knots (1.5 m/sec). Simultaneously, vertical sampling with Bogorov- Rass' net was carried out in order to determine the vertical distribution of *A. aurita* in the layer 0 – 100 m. The research demonstrated, that on average 2.6 % of total biomass of *A. aurita* was located in surface 5 m layer.

During 1989 – 2001 *A. aurita* and *M. leidyi* were sampled by the oblique sampling technique using Bongo net with diameter 61cm and vertically – using Bogorov-Rass' net.

Information about fisheries landings was compiled based on [32] and the FAO/GFCM database FISHSTAT http://www.fao.org/fi/struct/fidi.asp#FIDS [13]. Fish stock abundance assessments reported by [6, 10, 32, 36] and data of YugNIRO were used in the analyses. Population stability index for anchovy was estimated as $S=B_{min}/B_{max}$ [1], where B_{min} and B_{max} were the anchovy stock biomasses in May and November respectively according to [32].

Results. 1. Long-term plankton dynamics. The analysis of pelagic population data from the Black Sea revealed similar trends and correlations in various time-series [12]. Since the 1960s, the phytoplankton biomass tends to increase, and zooplankton – to decrease (Fig. 2). The biomass of the aborigine ctenophore *Pleurobrachia pileus* Fabr. increased in 1970s – to 1980s and decreased during the 1990s. All series presented clear decadal cycles with dominant periods of ~10 and ~ 20 years [12].

In the last 40 years the structure of the Black Sea mesozooplankton community changed greatly. The percentage of food organisms in the total mesozooplankton biomass in the 1960s was 37.5 %, in 1971 – 1975 – 32.2 %, and in 1988 – 1999 only 10.5 %. The share of the previously abundant *Cladocera* decreased greatly during the 1990s but showed signs of recovery in early 2000s. The copepod *Calanus ponticus* Claus, 1863 become dominant in the early 1990s, because of its ability to migrate to depths unreachable for *M. leidyi*.

Analyses of abundance and distribution of *A. aurita* started in late 1960s [28]. The analysis of distribution and abundance data revealed a low frequency cyclic dynamics of *A. aurita*. The highest density and biomass were observed in the shelf areas and in the Northwestern Black Sea (Fig. 3). The maximum abundance was observed during the 1970s until the late 1980s (Fig. 3). During the 1990s the population abundance was low, being coincident with the period of introduction and outburst of *M. leidyi* (Fig. 4).

Despite of differences in estimated absolute biomass of *M. leidyi* by different authors [5, 22, 50, 52] it should be admitted that *M. leidyi* was well established in the plankton community of the Black and Azov Seas. The spatial distribution of abundance (Fig. 4, 5) revealed that *M. leidyi* is more abundant in the shelf areas and over the years in the Northwestern Black Sea. However, in 1991 the biomass is almost equally abundant on the West as well as on the East of the Sea. Summer biomass (August) is much higher than the June spring one which revealed the dependence of *M. leidyi* on warm water and summer stratification. These characteristics of *M. leidyi* could also be related to the vertical distribution of the biomass (Fig. 6) which reveals a preference for the upper layer (also [25]).

In 1995, an attempt was made to study the vertical distribution of *A. aurita* and *M. leidiy* (Fig. 6). *M. leidyi* expressed preference for the upper warmed layer, down to depth 12 – 18 m, while *A. aurita* was distributed down to 100 m. The analysis of materials during the next years (1996 – 2001) presented evidence that the main factor determining the vertical distribution of the ctenophore during the year was the water temperature. The highest biomass of *M. leidyi* was observed in layers with the higher temperature and with a pronounced temperature gradient between the layers. The contrast in ctenophore vertical distribution became more distinct with strengthening the thermocline.

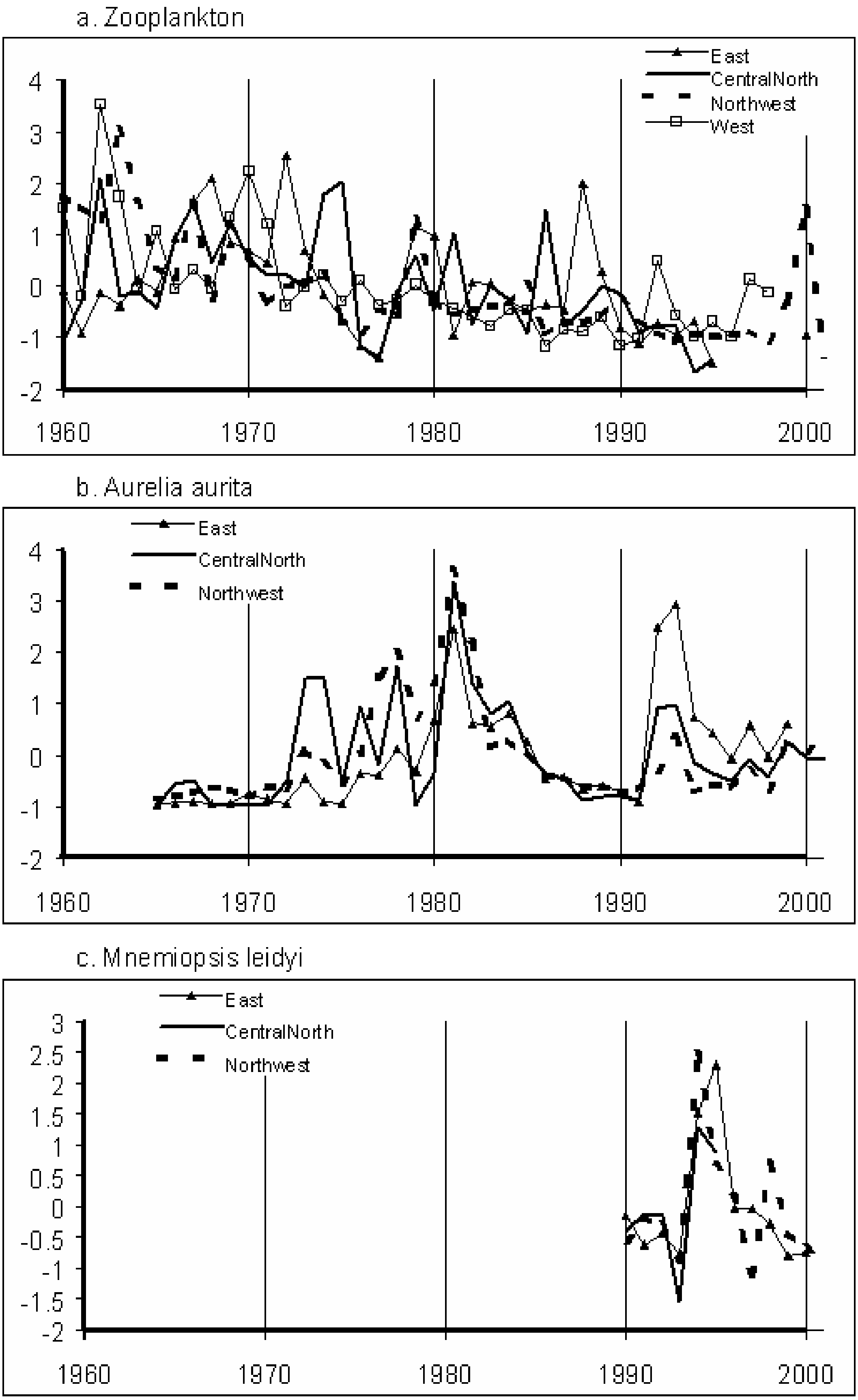

Fig. 2 Time-series of zooplankton biomass. Data are standardised to zero mean and unit variance.

Рис. 2 Временные ряды биомассы зоопланктона. Данные представлены в виде значений вариаций от среднего.

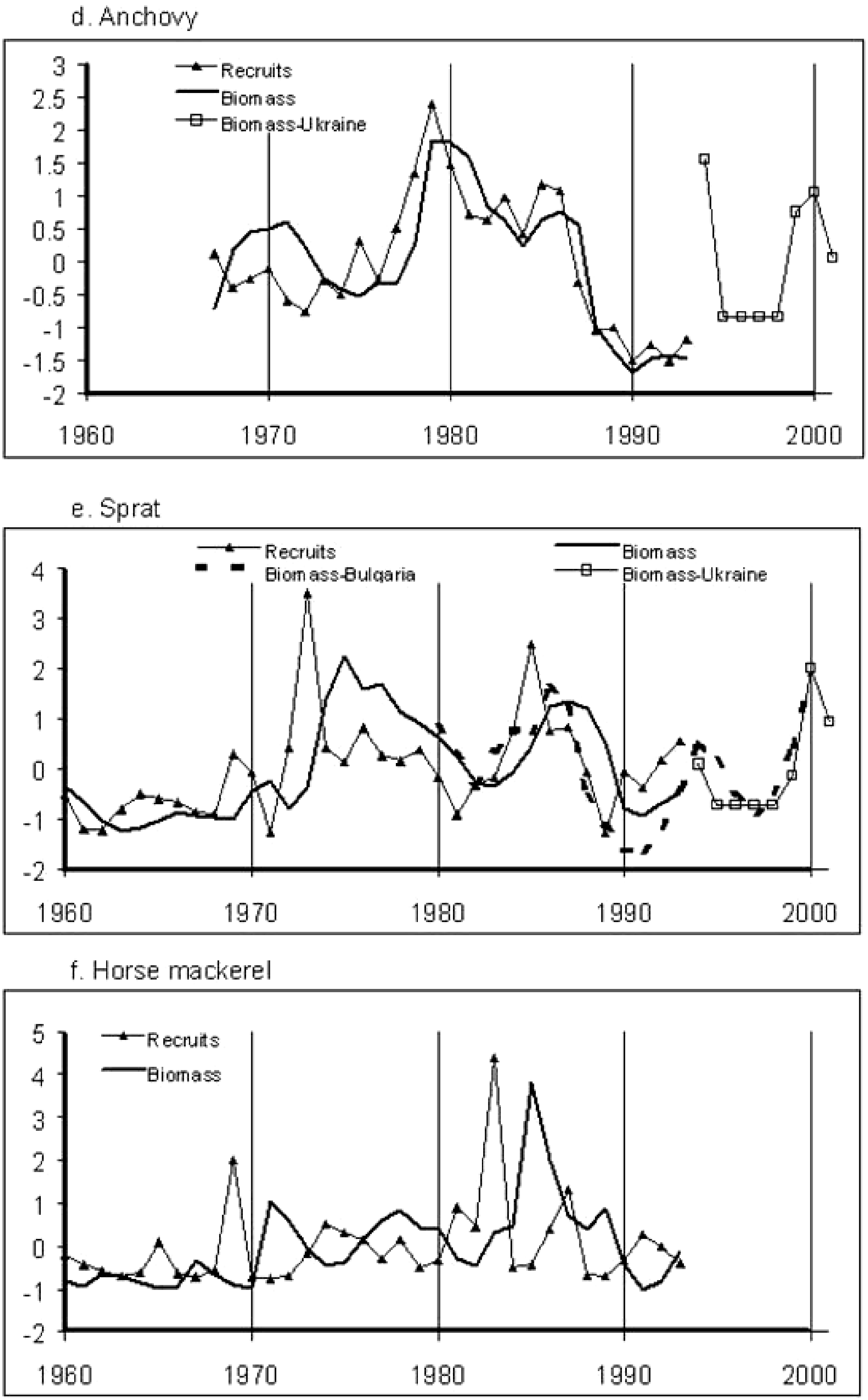

Fig. 2 (Contd). Time-series of abundance of the main commercial fish stock:
d. Anchovy,
e. Sprat,
f. Horse mackerel

Рис. 2 (Продолж.) Временные ряды биомассы зоопланктона. Данные в виде значений вариаций от среднего.

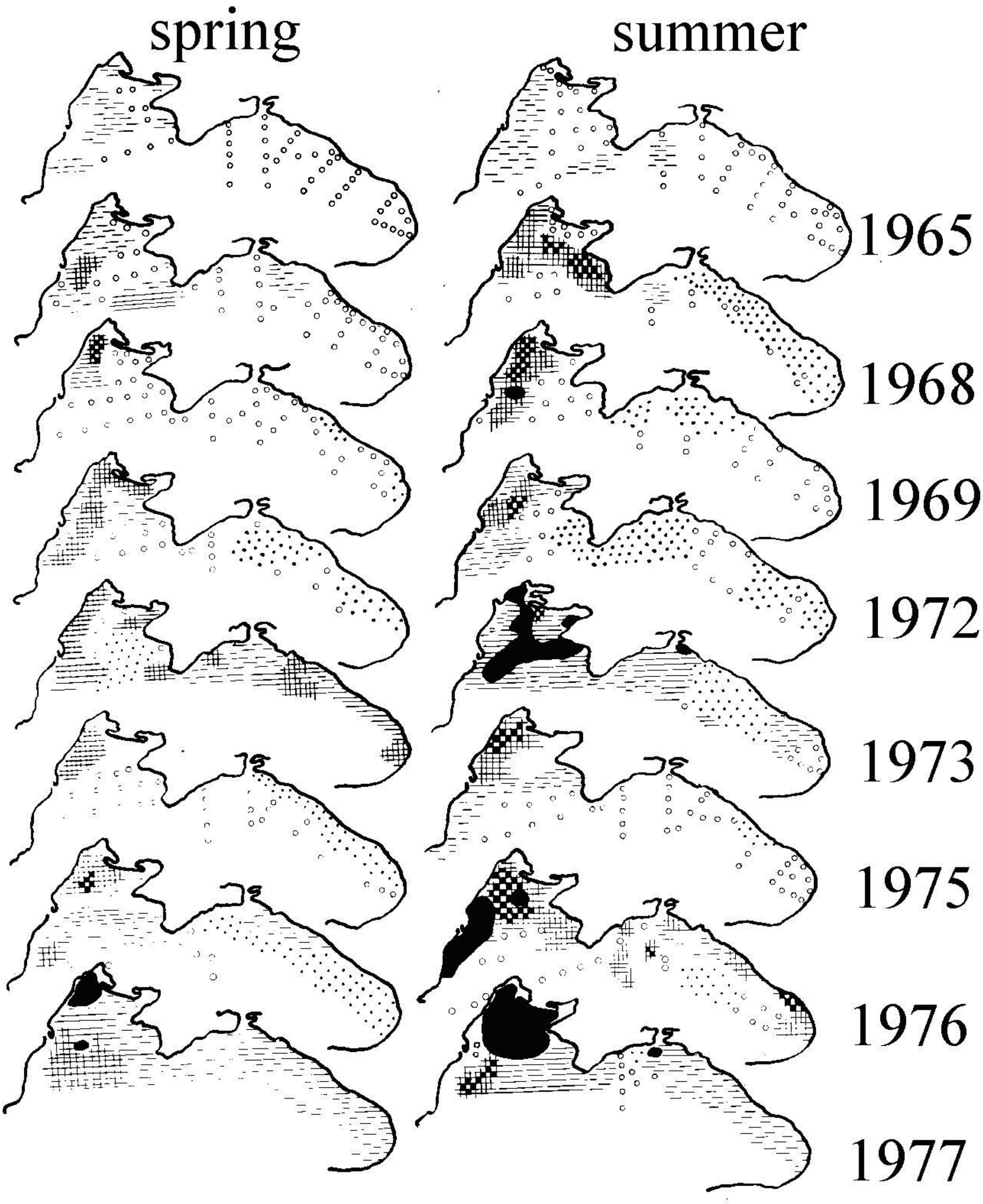

Fig. 3 Spatial distribution of the *A. aurita* biomass (kg) in the Black Sea
Рис. 3 Распределение биомассы (кг) *A. aurita* в Чёрном море

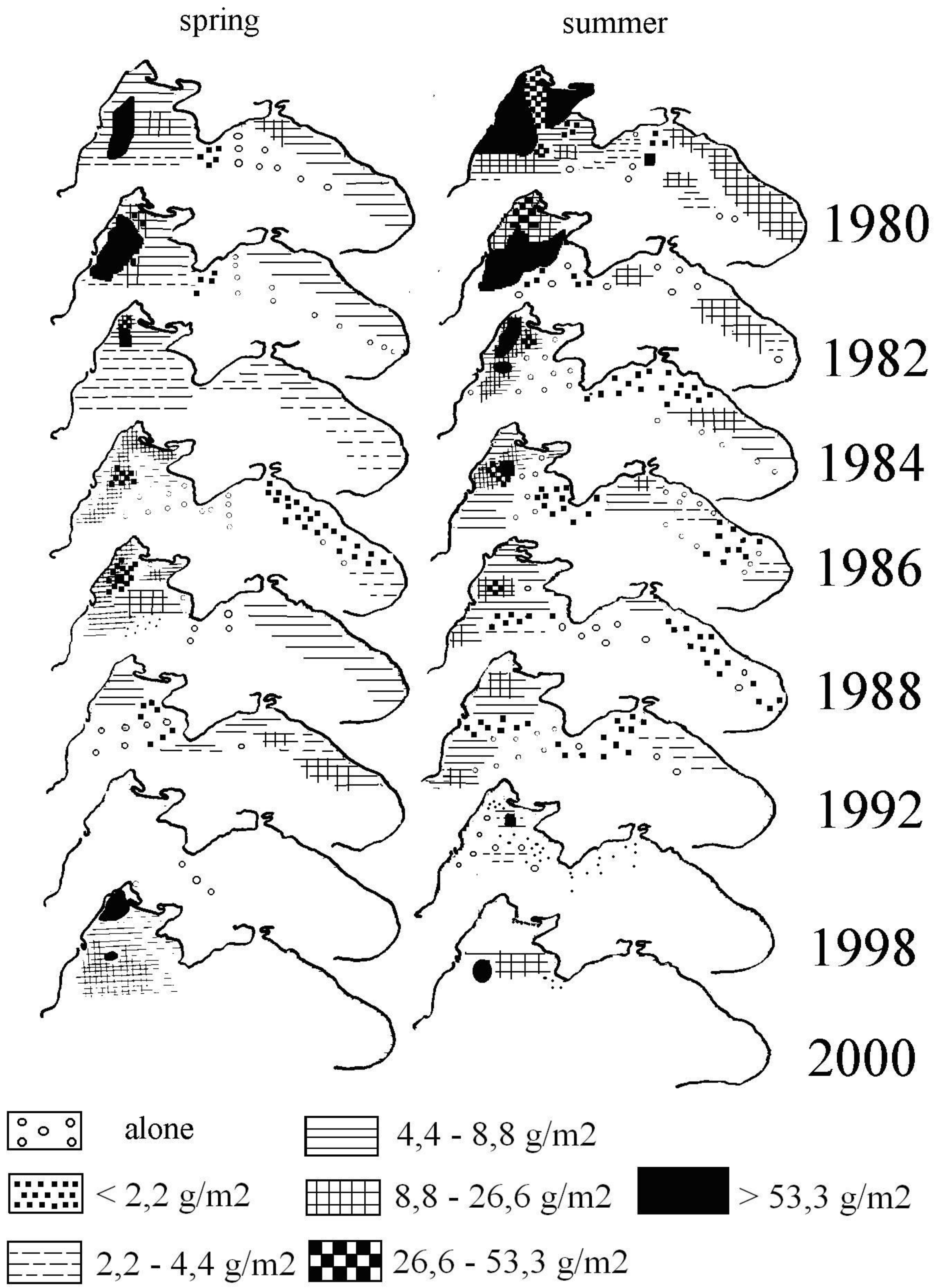

Fig. 3 (Contd). Spatial distribution of the *A. aurita* biomass (kg) in the Black Sea
Рис. 3 (продолж.) Распределение биомассы (кг) *A. aurita* в Чёрном море

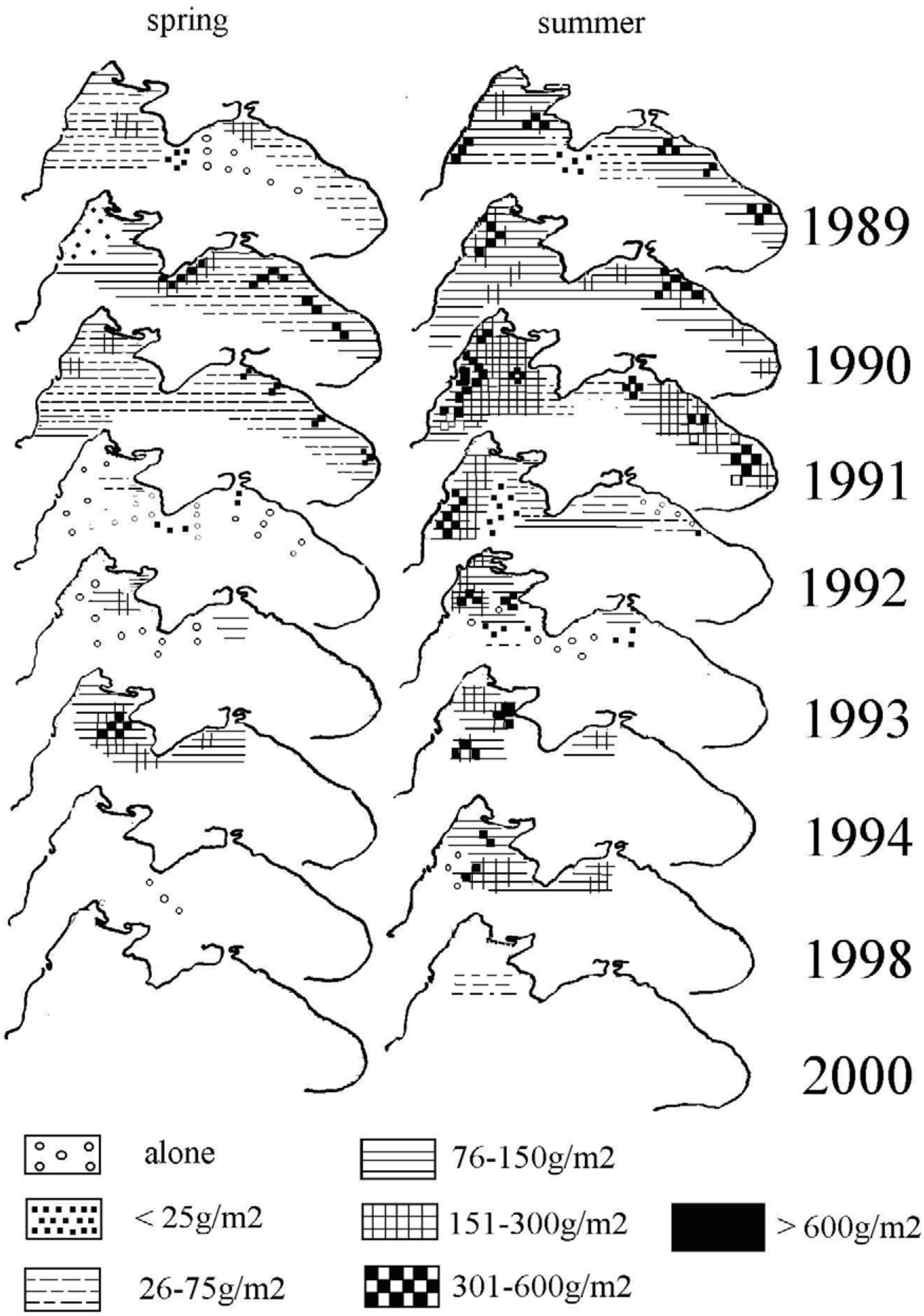

Fig. 4 Spatial distribution of the *M. leidiy* biomass (g.m^2) in the Black Sea
Рис. 4 Распределение биомассы (г.м^2) *M. leidiy* в Чёрном море

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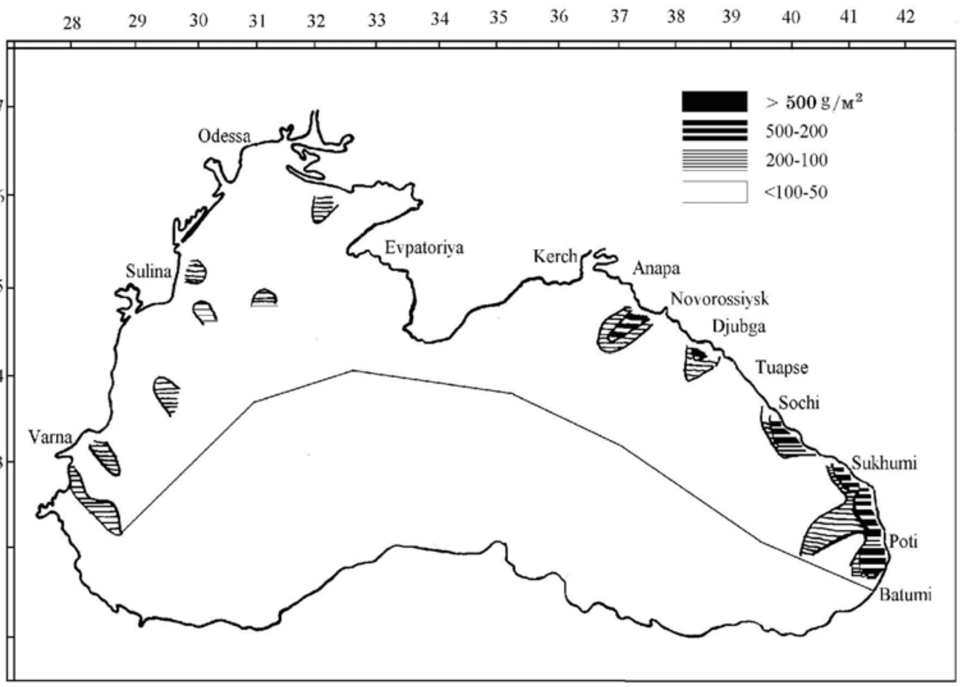

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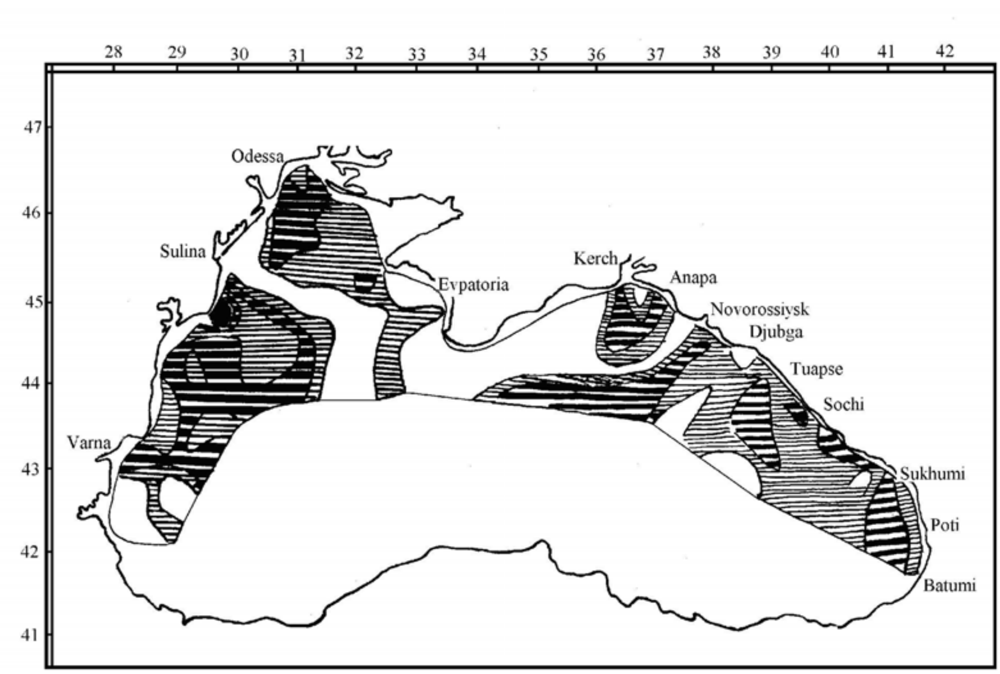
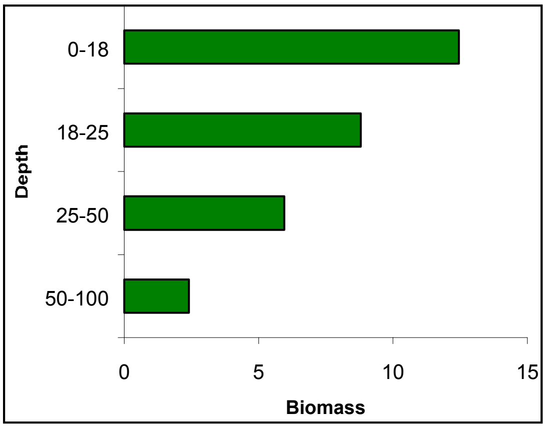


Fig. 5 Distribution of ctenophore *M. leidiy* biomass (g/m^2) in June and August 1991
Рис. 5 Распределение биомассы (г.м^2) *M. leidiy* в июне и августе 1991 г.



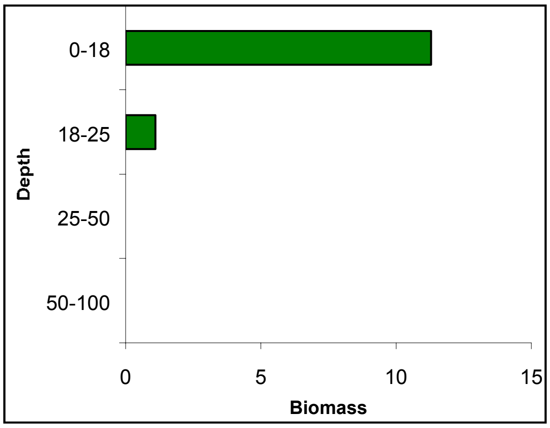
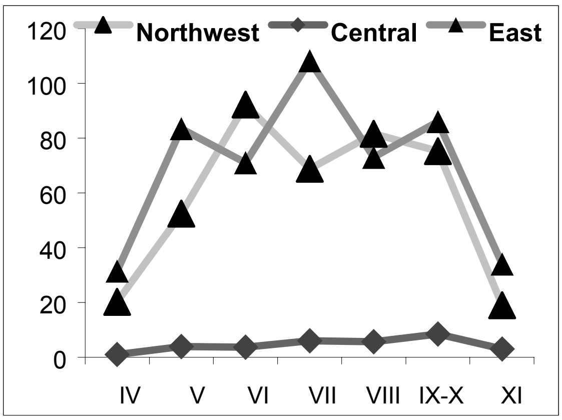


Fig. 6 Vertical distribution of gelatinous plankton biomass (g.m^{-3}) in the Black Sea
Рис. 6 Вертикальное распределение биомассы (г.м$^{-3}$) желетелого планктона в Чёрном море

It is interesting to compare the abundance of *M. leidyi* and that of its zooplankton food in several sites near the coast (3 miles offshore, Fig. 7). In April-May there was an abundant reserve of zooplankton food. Zooplankton was more abundant in the North and Southeast and an inverse relationship between *M. leidyi* abundance (which is generally low) and zooplankton can be observed across sites. However the inverse correlation (r = - 0.54) was of low statistical significance (and may be spurious), because of the low abundance of *M. leidyi* and thus the relatively low predation impact. In June-July the biomass of *M. leidyi* increased and that of zooplankton decreased. Inverse relationship was observed in Varna, Odessa, Kerch and the eastern sites, but in some other places (Constanta, Evpatoriya, Yalta) both zooplankton and *M. leidyi* abundance were low. The low zooplankton biomass might be due to predation of other zooplanktivores (e. g. fish) or some other factors (e. g. weather, currents). When the ctenophore biomass reached maximum in August the inverse relationship with food zooplankton became evident: r = - 0.73 p< 0.01. As on Fig. 6 the greatest abundance is recorded on the West and East of the Sea. The seasonal maximum of both *A. aurita* and *M. leidyi* are in Summer but high abundances were recorded also in late spring (May) and early autumn (Fig. 8).



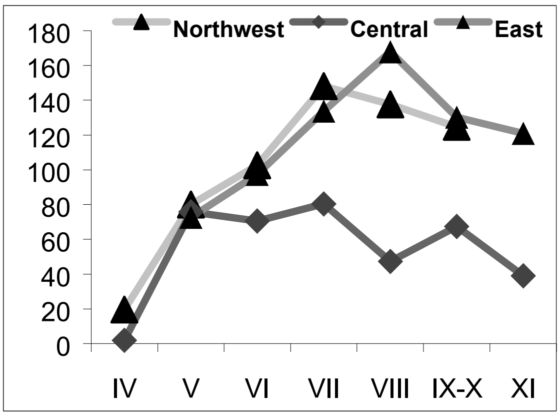


Fig. 8 Average (1990-2000) seasonal variation of gelatinous plankton biomass (g.m^{-2}) in the Black Sea
Рис. 8 Средние (1990 – 2000 гг.) сезонные вариации биомассы (г.м$^{-2}$) желетелого планктона

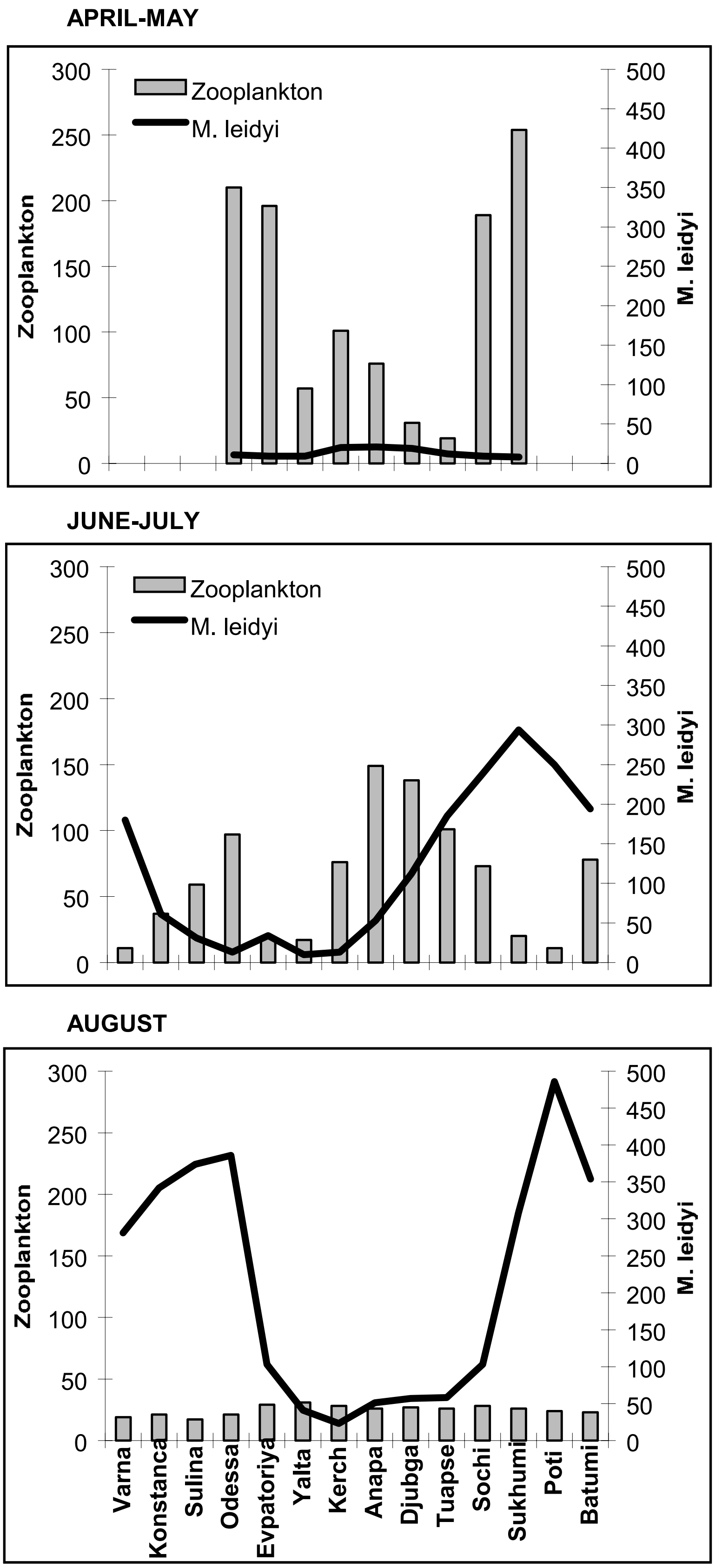


Fig. 7 Biomass of feed zooplankton (mg.m^{-3}) and *M. leidiy* (g.m^{-2}) in the vicinity of large ports (3 miles offshore) in the Black Sea in April-August 1991

Рис. 8 Биомасса кормового зоопланктона (мг. m^{-3}) вблизи больших портов (в 3 милях мористее) в Чёрном море в апреле – августе 1991 г.

Abundant development of the invader resulted in reduction in biomass not only of forage mesozooplankton, but also of the food competitor *A. aurita* [50]. The depression of *A. aurita* coincided with the period of introduction of *M. leidyi* (Fig. 2). In 1993 the sharp reduction in *M. leidyi* abundance in the Black Sea was accompanied by a general increase in *A. aurita.* In 1994 an outburst of *M. leidyi* was registered corresponding to reduction of *A. aurita*. After 1996 *A. aurita* population progressively increased contrary to the reduction of *M. leidyi* which in recent years was possibly negatively impacted by its predator – the exotic ctenophore *Beroe ovata* (Branguiere 1789) [43, 19].

2. Some experimental studies: reproduction and feeding

The present-day understanding of the annual reproduction cycle of *M. leidyi* in the Black Sea is based on studies of the dynamics of size composition. *M. leidyi* is thought to reproduce during the whole year, as evidenced by the almost permanent presence of juveniles less than 10 mm. As the juveniles are most abundant during the summer months, it is believed that reproduction peaks in July-August, while the minimum is in late April-early May [41]. Assuming such as reproduction pattern and considering that *M. leidyi* reaches a size of 10 mm in ten days, it can be supposed that a reproduction peak always precedes the biomass maximum in late summer and autumn. However some observations showed, that intense reproduction may also happen in spring or autumn.

The rate of daily food consumption by *M. leidyi* was first evaluated in the year after its massive outbreak in the Black Sea in 1988 [50]. Both direct and indirect methods for calculation were used [16, 17, 18]. It appeared from laboratory observations [20] that average daily ration of a specimen of 15 mg of carbon body weight was equal to 7 % of its body weight, whereas the indirect method using the average daily exchange rate yielded in smaller values – 1-5 %. A similar approach was used by Tsikhon-Lukanina et al. [48, 49]. As in the previous case, the authors experimented mostly with *Calanus*, which was, made available to the ctenophore in concentrations of 4 to 66 ind.l^{-1}. The daily ration of *M. leidyi* individuals with average body mass as in the previous experiment was estimated as 3,3% at food concentration of 1460 mg.m^{-3}. The ctenophore actually ceased to feed on *Calanus* concentrations less than 600 mg.m^{-3} or 3 ind.l^{-1}.

It should be noted that although fish larvae are part of the diet of *M. leidyi* [47, 48, 49] they are only a very little percentage and the consumption of fish larvae by *M. leidyi* hardly can lead to fish recruitment failure and fisheries collapse as stated in some earlier works. Though the trophic effect of *M. leidyi* on fish stock should be realised through feeding competition.

3. Fisheries development

The fisheries development in the Black followed the classical boost-and-crash scheme (Fig. 9). Untill the early 1970s the main target were the large and mid-size predatory pelagic and demersal species like bonito, bluefish, mackerel, turbot until those stocks severely declined [11, 32]. The fishing effort sharply increased in the 1970s and 1980s with the introduction of large-scale purse seine (Fig. 10) and mid-water trawl fisheries of small pelagic fish (anchovy, sprat, horse mackerel). In the mid 1980s the total catch reached near 800 thousand tonnes, about 65 % of which was anchovy and about 20 % sprat and horse mackerel [32]. A synchronous decrease in all stocks by the late 1980s (Fig. 9) [32] created hard socio-economic problems for the fisheries. The catches of anchovy and other small pelagic fish decreased with more than a factor of 5 and reached levels of ~ 100 000 tonnes – similar to those during the pre-development period.

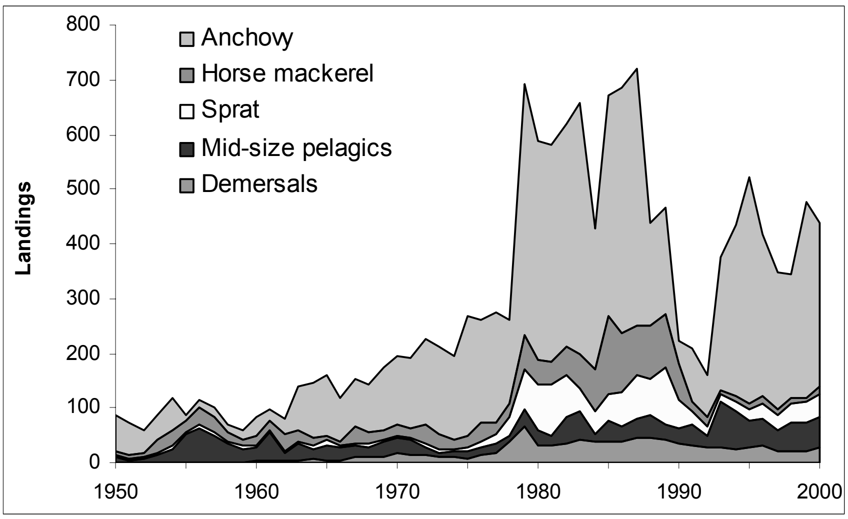


Fig. 9 Fish landings in the Black Sea

Рис. 9 Вылов рыбы в Чёрном море

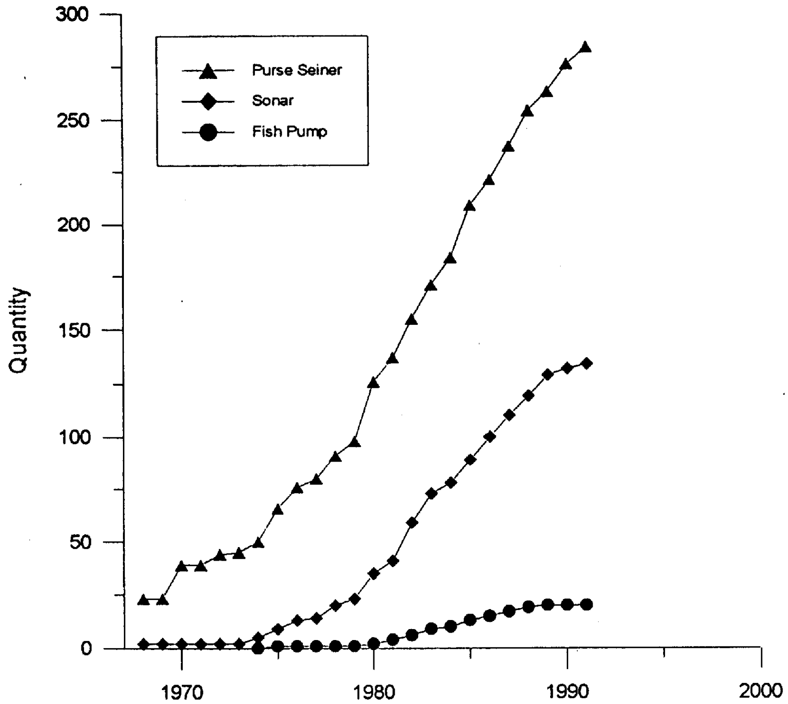


Fig. 10 Increase of fishing effort in Turkey (from Gucu, 1997)

Рис. 10 Рост рыболовного усилия в Турции (из Gucu, 1997)

4. Main fisheries stocks and possible effects of gelatinous zooplankton

Anchovy *Engraulis encrasicolus ponticus* Alexandrov, 1927 is the most abundant fish in the catch in the last decades [13, 32]. During the years 1974 to 1980, anchovy catches increased, from 152 to 460 thousand tons, with major contribution to the total catch by Turkey and the former USSR.

The anchovy stock (largely constituted by juveniles of age 0.5 year) showed upward trend in abundance during that period, increasing from 800 to 1600 – 1800 thousand tons [32]. The rate of removal did not exceed 50 % of the stock. In the subsequent years until 1991 there was a steady downward trend in the anchovy stock (Fig. 2). In 1990 the anchovy stock was below 300 thousand tons – the lowest level over the period 1967 – 1993. YugNIRO assessment results showed that after the 1981/82 fishing season the limit fishing mortality for safe exploitation ($F_{0.1}$) has been systematically overrun [37], causing a average annual reduction of 7 % over 1981 – 1986. By 1987 the anchovy stock was reduced to 900 thousand tons, still remaining high enough to support an annual catch of 400 thousand tons. The high catches were maintained by the relatively large reproductive stock. First signs of overfishing appeared after 1984 [37] when anchovy shoals were difficult to be found and the fishery enterprises incurred losses. However, the real catastrophe happened after 1986, when in two subsequent years the stock shrunk from 1200 to 500 thousand tons. Catches during the 1986/87 and 1987/88 remained high, at the level of 452 – 469 thousand tons, but in the following 1988/1989 fishing season the catch suddenly dropped to 188 thousand tons. The annual rate of stock reduction was 25 % for 1987 and 44 % for 1988 on average 29 % for 1987-1988. In these years the initial outbreak of *M. leidyi* was reported in the Black and Azov Seas. It is obvious that the catastrophic reduction of the Black Sea anchovy stock in the late 1980s was due to the combined action of two factors: the excessive fishing and *M. leidyi* outburst. Assuming the anchovy stock reduction rate due to overfishing to be the same as the average for the period 1984 – 1987 (14 %), it appears then during 1988 the *M. leidyi* impact on the anchovy stock was about two times (30 % reduction rate) greater than the influence of overfishing [23]. Since 1988 catches of the Black Sea anchovy remained below the multiannual average. During the 1990/1991 fishing season an unprecedented situation arose: no fishable aggregations were found off Georgia and the catch was only 2.3 thousand tons. The fat content was by 40 – 60 % lower than in the previous years [33]. Fishing situation off Anatolian coast was also extremely bad: Turkish catches were 73 thousand tons in the 1990/1991 comparable to the level of the early 1970s when the fishing power was much less.

The total loss from the anchovy catch over the years 1989-1992 due to *M. leidyi* outbreak can be roughly estimated of about 1 million tons.

In the subsequent years 1993 – 1996 following the disintegration of the Soviet Union neither large-scale purse seining for anchovies nor YugNIRO fisheries research in the South-Eastern Black Sea were conducted, so it is difficult to judge the real state of the Black Sea anchovy resource in these years. Turkish catches of anchovy off the Anatolian coast in the years 1993, 1994, 1995 and 1996 were 218.9; 278.7; 377.8 and 273.2 thousand tons respectively, indicating certain recovery of the Black Sea anchovy stock since 1992. The YugNIRO hydroacoustic surveys in the Georgian waters during the 1997/1998 – 2003/2004 also presented evidence of the satisfactory state of the anchovy stock.

Damage by *M. leidyi* to the anchovy population is most likely done through food competition, as unusually low levels of the summer food zooplankton have been observed in the top 50 m layer over the period studied. Anchovy larvae could be also affected by predation by *M. leidyi*. Mass appearance of anchovy larvae in the plankton occurs in July and August, coincident with the seasonal peak of *M. leidyi* biomass. *M. leidyi* is capable to consume a daily ration several times greater than its own weight [15, 27]. Its food spectrum is quite wide and includes fish larvae [47]. There is an overlap in the distribution of anchovy larvae and *M. leidyi*, however, anchovy larvae are predominantly found in the narrow coastal zone, while the ctenophore is also distributed further offshore.

After the population collapse following the intrusion of *M. leidyi*, the Black Sea anchovy population has become adapted to the new conditions in its spawning and feeding areas. The dynamics of stability coefficient (Fig. 11) showed a decrease in stability only during the initial years of the *M. leidyi* invasion.

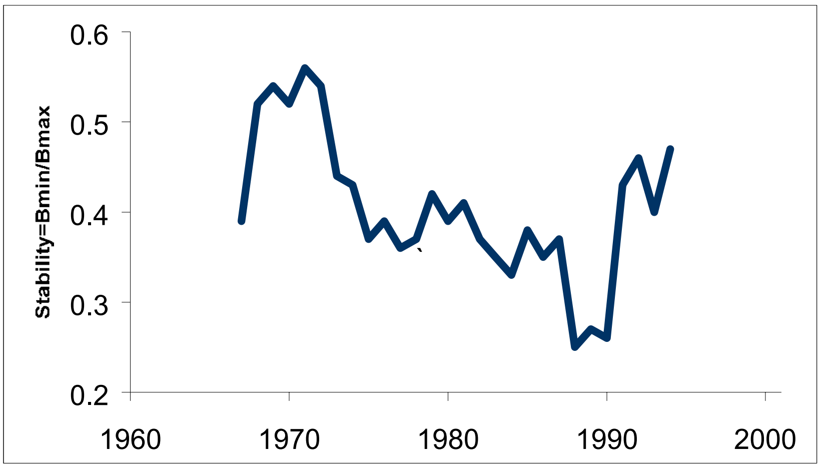


Fig. 11 Temporal dynamics of the stability index (B_{min}/B_{max}) of anchovy

Рис. 11 Динамика индекса стабильности (B_{min}/B_{max}) у анчоуса

After 1991 the recruitment and individual growth and condition were high, that led to increased population growth during the summer season and relatively quick recovery of the stock.

However there is no guarantee against a repetition of such catastrophic reduction of the anchovy stock. In fact the current research does not provide an answer of the question: what precautionary limit level of removal from the stock and hence total allowable catch (TAC) must be set on the anchovy fishery, considering the deleterious effect of *M. leidyi.* The sad experience from the 1980s has shown that anchovy catches, however high and stable for a few years, may not be an indication of the anchovy stock stability; because with high *M. leidyi* levels present, the stock may be depleted in one or two fishing seasons.

Although *M. leidyi* outbreak in the Black Sea has affected all components of the ecosystem and populations of pelagic zooplanktivorous fish in particular, the latter were differently affected. Whereas warm-water anchovy inhabits together with *M. leidyi* the top 50m layer, the cold-water sprat *Sprattus sprattus phalericus* (Risso, 1826), capable of feeding and spawning in deeper layers presented somehow different dynamics (Fig. 2). The sprat spawning takes place during the winter and spring when *M. leidyi* biomass and its impact on the fish food supply are relatively low. In summer, the juvenile and adult sprat leave the upper warmed layer and thus avoid severe competition for food with other plankton-eaters including *M. leidyi*. During this period their preferred food consists mainly of the cold-water *Calanus* and *Pseudocalanus* copepod species. It should be noted that this prey is also available to *M. leidy*, as these species migrate to the thermocline boundary at night when they can be eaten by the ctenophore which has a daily feeding maximum at this time. This can partly explain some decrease of the sprat stock in the late 1980s (Fig. 2). After 1992 the stock already recovered and recently the catches also started to increase [13].

Unlike *M. leidyi*, *A. aurita* is distributed in deeper water (Fig. 6) and more trophic interference with sprat may be assumed. It seems that the peak in *A. aurita* abundance corresponded to a decrease in sprat recruitment and biomass (Fig. 2) [12]. A negative effect of the outburst of *A. aurita* and *M. leidyi* on sprat growth and condition has also been hypothesized [39]. The outbursts of gelatinous plankton produced a bulk of organic material unutilised by higher trophic levels (gelatinous plankters are dead-ends in the food chains), which greatly contributed to the detritus pool and after being decomposed led to increase in bottom hypoxia and anoxic production of hydrogen sulphide on the shelf [53]. Most of the demersal organisms (but not larval jellyfish which is resistant to low oxygen) and some pelagic ones distributed in deeper waters like sprat and the aborigene ctenophore *P. pileus*, apparently suffered from the increased levels of hypoxia and hydrogen sulphide [12].

The horse mackerel *Trachurus mediterraneus ponticus* (Aleev, 1956) fishery operates mainly on the wintering grounds in the southern Black Sea using purse seine, mid-water trawl and cone nets. The horse mackerel of age 1 – 3 years generally prevails in the commercial catches, but strong year classes (for example, the 1969-year class) may enter into exploitation at age of 0.5 year and may prevail up to age 5 – 6 years. Over the last 40 years, highest horse mackerel catches were reported in the years preceding *M. leidyi* outbreak in 1988 and during the two following years 1989 – 1990 [13, 32]. The maximum catch of 141 thousand tons was recorded in 1985, from which ~100 thousand tons were caught by Turkey [32]. In the next four years catches remained at the level of 97 – 105 thousand tons. In the period 1971 – 1989, the stock increased, although years of high abundance alternated with years of low abundance due to year classes fluctuations, typical of this fish. VPA estimates showed that the stock was highest in 1984 – 1986 (Fig. 2) [32]. Scientists [2, 6] believed that the intensive fishing in Turkish waters in 1985 – 1989 led to overfishing of horse mackerel population and reduction of the stock and catches in the next years. A drastic decline of the stock occurred between 1986 and 1990. In 1991 the horse mackerel stock dropped to a minimum of 75 thousand tons and the catch dropped to 4.7 thousand tons, that is a twenty fold reduction compared to the average annual catch in 1984 – 1986.

In contrast to anchovy and sprat, the horse mackerel stock still remains in a depressed state. There was no fishing for horse mackerel by the former USSR countries in 1992 – 1998 because no fishable aggregations were found on the wintering grounds. Small quantities of horse mackerel were caught with trap-nets in the coastal areas of the Crimea and Caucasus. In Turkish waters, horse mackerel catches in 1994 – 1996 were 9 – 11 thousand tons, i. e. at the level of the years 1950 – 1975 before the start of industrial fishing.

During 1985 – 1993, only in 1988 a relatively successful recruitment was recorded. Despite of its coincidence with the first year of *M. leidyi* outbreak, the juveniles from this cohort were sufficiently well supplied with food. As the first burst of *M. leidyi* occurred in the autumn of 1988, the summer zooplankton maximum production did not suffer much from the devastating effect of *M. leidyi*. The copepods *Oithona nana* Giesbr., 1892 and *Oithona similis* Claus, 1963 which constitute the main food of larval horse mackerel [34], were especially abundant. However, the favorable trophic conditions for larvae in summer 1988 failed to ensure the formation of numerically strong year-class because further in the year juveniles were faced with strong feeding competition with *M. leidyi*. Sharp decline of *Oithona* under the predation pressure of *M. leidyi* in the subsequent years [40, 53] affected the survival of horse mackerel. Dietary studies of juvenile and adult horse mackerel [27] have shown that both the habitat diet of juvenile horse mackerel and *M. leidyi* overlap, therefore the strong feeding pressure by *M. leidyi* on zooplankton directly affected larval and juvenile horse mackerel.

In addition to the most abundant stocks reviewed in the above paragraphs almost all fish stocks decreased synchronously in the early 1990s. As fish larvae are pelagic and feed on zooplankton this effect can partially be contributed to the drastic decrease in zooplankton food associated with *M. leidyi* but overfishing was also reported of being playing a significant role [32].

Discussion. Gelatinous plankton outbursts should be interpreted in the context of the overall Black Sea ecosystem change because of the complex direct and indirect effects on structure and productivity they are believed to produce.

During the 1970s and 1980s a general increase in biological productivity was observed, that could be related to variation in hydroclimate and cultural eutrophication [12]. A long-term decline in SST (sea surface temperature) after 1965 may be responsible for increased upper layer instability and convection (most important in winter). This process intensifies divergence (upwelling) and mixing in the central zone and over the shelf [30], leading to enrichment of nutrients in the photic layer. An increase in run-off, which peaked around 1980, may also have favoured increased productivity.

Zooplankton biomass was positively correlated with SST and exhibited an inverse trend with respect to phytoplankton and pelagic fish. This may be related to a temperature effect on zooplankton growth or may be caused by a trophic cascade effect of increased zooplanktivory by fish and gelatinous zooplankters. According to [11, 12], overfishing of marine predators provoked cascading changes resulting in increase of planktivorous fish and jellyfish, decrease in zooplankton and increase in phytoplankton during the 1980s comparing to the 1960s. Elimination of mackerel, which feed on *A. aurita* [53], could also favour the cascade increase in jellyfish.

Before 1970 there were no records of substantial jelly-plankton outbursts and the first biomass estimates ware relatively low [28], although the sampling gear – a commercial trawl) was not very reliable. The first records of jellyfish outbursts dated from the early 1970s (*Rizostoma pulmo* Macri, 1778, *A. aurita)* were related to the increased eutrophication [55]. Later development (Table 1) created for the Black Sea the glory of a sea of jellies. The causes and effects of gelatinous plankton outbursts should clearly be searched at ecosystem level (Table) [11, 12, 23,43].

The well documented invasion of *M. leidyi* and its consequences for fish stocks can be viewed as an example of interactions between natural and anthropogenic factors creating several feedbacks et ecosystem level. In the 1980s, the system was dominated by small pelagic fish and jellyfish *A. aurita*. After 1985 the jellyfish

A. aurita was replaced by the alien ctenophore *M. leidyi* in terms of biomass dominance [20]. The boom of *M. leidyi* in 1989 and 1990 corresponded with a decrease in abundance in most fish stocks. The causes of the exact timing of the *M. leidyi* onset are not clear, but decreased planktivory caused by low abundance of fish stocks (and overexploited stocks especially) may be one of them [12, 20, 32]. The fast development of *M. leidyi* in subsequent years led to a great decrease in zooplankton and strong competition for food with fish and aboriginal jelly-plankton (Table 1) [20, 36]. It is possible that the fishery collapse is not the only large negative consequence of the *M. leidyi* invasion, but that massive phytoplankton blooms by the late 1980s – early 1990s can be associated with a decrease in zooplankton grazing and a trophic cascade similar to that of the 1970s – 1980s [11].

Table 1 Summery of evidence of gelatinous plankton outbursts in the Black Sea and their effects on fish stocks and other components of the Black Sea ecosystem
Табл. 1 Влияние желетелого планктона в Чёрном море на запасы рыб и другие компоненты черноморских экосистем

Time	Event	Effects, comments	References
1950s-1960s	Low abundance of *A. aurita*	Low consumption and high biomass of zooplankton	[10, 14, 22]
About 1970 Early 2000	Outbursts of jellyfish *R. pulmo*	Related to the increased eutrophication; Damage fishing nets and catch	[45]
1970s-1980s	Increased biomass of *A. aurita* peaked about 1980	Substantial consumption of zooplankton, structural changes in the food web, large production of detritus leading to increased hypoxia, hypothetical negative effect (through competition for food) on planktivorous fish stocks, mechanical damages in fisheries	[10, 11, 14, 31, 32, 36, 45]
1970s-1980s	Increased biomass of the aboriginal ctenophore *P. pileus*	Increased consumption of zooplankton	[10, 11]
Late 1980s-1990s	Decrease in *A. aurita*	No change in zooplankton. Decrease partly due to *M. leidyi* invasion but can also be due to changes in hydroclimate and eutrophication	[11]
1990s	Decrease in *P. pileus*	Can be related to competition with *M. leidyi*	This article
1990s	Unintentional introduction and outburst of *M. leidyi*	Strong decrease in zooplankton and cascade changes in phytoplankton; collapse of almost all fish stocks under combined action of overfishing and *M. leidyi*; Competitive decrease in other zooplanktivores: *A. aurita, P. pileus*, *Sagitta cetosa* (Muller, 1847), Increase in detritus	[14, 40, 45]
Late 1990s	Unintentional introduction of *B. ovata*	Hypothetical predatory effect on *M. leidyi* and consecutive structural cascade changes in zooplankton ant its consumers including fish	[20, 35]
Early 2000	Relative decrease in *M. leidyi*	Can be related to predation by *B. ovata* and general adaptation of the system e.g. recovery of planktivorous fish	This article
Early 2000	Anecdotal increase in *R. pulmo*	Could be related to relative decrease in *M. leidyi* and available zooplankton food and /or change in hydroclimate (increase in temperature)	This article

The introduction of *B. ovata* [26, 43] was supposed to lead to further structural changes and possibly to control of *M. leidyi* and further recovery of fish stocks. Although the leading factor for fish stock reduce is now recognized to be the overfishing, *M. leidyi* outburst being an associated factor, and the recovery of certain stocks (anchovy, sprat) took place after the decrease in fishing pressure.

Conclusion. Ours first results suggested that gelatinous plankton outbursts resulted in structural and functional transformations in the ecosystem including direct and indirect effects on both pelagic and demersal habitats. Fish stocks were affected mainly by food competition through decimation of the food zooplankton. Although fish larvae are part of the diet of *M. leidyi* they make only a very little percentage and their consumption which hardly can lead to fish recruitment failure and collapse. The collapse of the fisheries in early 1990s was mainly due to severe overfishing by unregulated fisheries (anchovy and horse mackerel), although *M. leidyi* invasion also negatively contributed by decimating the zooplankton food reserve. Apart of its direct effects on zooplankton gelatinous plankton also produced important indirect effects leading to increase in phytoplankton and detritus and further leading to reduced water quality, hypoxia and hydrogen sulphide production and their harmful effects on fishes and other organisms.

1. *Alimov A. F.* An Introduction to Production Hydrobiology. – L., 1989. – 150 p. (in Russian).
2. *Bryantsev V. A., Serobaba I. I., Shlyakhov V. A., Yakovlev V. N.* Biological resources of the Black Sea in the present ecological conditions Ed. Prof. K.C. Guven // Proc. of the Black Sea Symp. Ecological Problems and Economical Prospects. – Istanbul: Acar Matbaacilik A.S., 1994. – P. 293-296. (in Russian).
3. *Bryntseva Yu. V., Bryantsev V. A., Kovalchuk L. A., Samyshev E.* Z. Relationship of biomass dynamics of diatomaceous and Peridinea Black Sea algae and atmospheric transfers // Hydrobiological Journal of Ukraine NAS. – Kiev, 1997 – 18 p. - DSU in VINITI 21.04.97, No 1309 B97. (in Russian).
4. *Caddy J. F., Griffiths R. C.* A perspective on recent fishery-related events in the Black Sea // Studies and Reviews. – GFCM. 63, FAO, Rome. – 1990. – P. 43-71.
5. *Chashchin A. K., Grishin A. N., Dubovik V. E.* Interannual and seasonal dynamics of ctenophore *M. leidyi leidyi* development and its impact on resources of the pelagic fishes in the Azov and Black Seas // Proc. of the Southern Scientific Research Institute of Marine Fisheries & Oceanography. – Kerch: YugNIRO, 1996. – **42**. – P. 162-167. (in Russian).
6. *Chashchin A. K.* The anchovy and other pelagic fish stocks transformations in the Azov-Black Sea basin under environmental and fisheries impact // Proc. 1st Intern. Symp. Fish. Ecol. – 1998. – P. 1 – 10. (in Russian).
7. *Danilevsky N. N.* Pelagic trawl for quantitative registration of juveniles // Rybnoye Khozyaystvo. – 1968. – No 10. – P. 25-26. (in Russian).
8. *Daskalov G.* Using abundance indices and fishing effort data to tune catch-at-age analyses of sprat *Sprattus sprattus*, whiting *Merlangius merlangus* and spiny dogfish *Squalus acanthias* in the Black Sea // Cah. Options Mediterr. – 1998. – **35.** – P. 215-228.
9. *Daskalov G. M.* Mass-balance modeling and network analysis of the Black Sea pelagic ecosystem // Izv. IRR, Varna, 2000. – P. 49-62.
10. *Daskalov G. M.* Population ecology and stock dynamics of the Black Sea sprat *Sprattus sprattus* // IFA annual report (mimeo). – 2001. – P. 2-6.
11. *Daskalov G. M.* Overfishing drives a trophic cascade in the Black Sea // Mar. Ecol. Prog. – 2002. – Ser. 225. – P. 53-63.
12. *Daskalov G. M.* Long-term changes in fish abundance and environmental indices in the Black Sea // Mar. Ecol. Prog.–2003.–Ser. 255. – P. 259-270.
13. *Fishery* information, data and statistics service (FIDS) // FAO Fisheries Department http://www.fao.org/fi/struct/fidi.asp#FIDS.
14. *Fashchuk D. Y., Samyshev E. Z., Shlyakhov V. A.* Forms of anthropogenic impact on the Black Sea ecosystem and its state in current conditions // Sea Ecology – 1991. – 38. – P. 19-28 (in Russian).
15. *Fashchuk D. Ya.* Hydrogen sulphide zone of the northwestern Black Sea shelf: Nature, origin, dynamics // Vodnye resursy. – Moscow, 1995. – **22**, No 5. – P. 568-584 (in Russian).
16. *Finenko G. A., Abolmasova G. I., Romanova Z. A.* Nutrition, oxygen consumption and growth of ctenophore Mnemiopsis mccradyi depending on food concentration // Sea Biology (Vladivostok). – 1995. – **21**, No 5. – P. 315-320. (in Russian).
17. *Finenko G. A., Romanova Z. A.* Population dynamics and energetic of ctenophore Mnemiopsis leidyi // Oceanology. – 2000. – **40,** No 5. – P. 720-728. (in Russian).
18. *Finenko G. A., Zomanova Z. A., Abolmasova G. I.* et al. Impact of nutrition conditions on the rate of food digestion and consumption rate of lobe ctenophore

Mnemiopsis leidyi// Mar. Ecol. J. – 2005. – **4,** No 1. – P. 75-83. (in Russian).
19. *Finenko G.A., Romanova Z.A., Abolmasova G.I.* et al. Ctenophora Invaders and Their Role in Trophodinamics of the Planktonic Community in the Costal Wathers of the Crimea Area of the Black Sea (Stvastopol Bay) // Oceanology. – 2006. – 46, No 4. – P. 507-517 (in Russian).
20. *Grishin A. N.* Dietary daily regime and food spectrum of ctenophore *M. leidyi* in the conditions of the Black Sea // Proc. of the Southern Scientific Research Institute of Marine Fisheries & Oceanography. – Kerch: YugNIRO, 1994. – **40**. – P. 45-47.
21. *Grishin A. N., Kovalenko L. A., Sorokolit L. K.* Trophic relations in Black Sea plankton communities before and after introduction of ctenophore *Mnemiopsis leidyi* (A. Agassiz) // Proc. Southern Scientific Research Institute of Marine Fisheries & Oceanography. – Kerch: YugNIRO, 1994. – **40**. – P. 38-43 (in Russian).
22. *Grishin A. N., Arkhipov A. G.* Some results of study of transformation of planktocenosis // Rybnoye Khozyaystvo. – 1995. – **4.** – P. 44-45 (in Russian).
23. *Grishin A. N., Shlyakhov, V. A.* On possibility of increase of the Black and Azov Seas fish productivity // Fish Industry of Ukraine. – 1999. – **4.** – P. 24-27 (in Russian).
24. *Grishin A. N.* Energetic balance and ecological efficiency of pelagic communities in the Black Sea // Hydrobiological Journal. – 2001. – **37**, No 6. – P. 3-10 (in Russian).
25. *Kideys, A. E., Romanova Z.* Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996-1999 // Marine biology. – 2001. – **139**, No 3. – P. 535-547.
26. *Konsulov A. S., Kamburska L. T.* Ecological Determination of the New Ctenophora. – *Beroe ovata* Invasion in the Black Sea // Oceanology. – Varna, 1998. – **2.** – P. 195-198.
27. *Lipskaya N. Ya., Luchinskaya T. N.* Biology of ctenophore *M. leidyi //* Rybnoye Khozyaystvo. – 1990. – **9.** – P. 36-38 (in Bulgarian).
28. *Mironov G. N.* Biomass and distribution of the jellyfish *Aurelia aurita* (L.) from trawl survey data in 1949-1962 in the Black Sea // Biologiya moray. – Kiev, 1971. – **24.** – P. 49-69 (in Russian).
29. *Niermann U., Kideys A. E., Kovalev A. V.* et al. Fluctuations of pelagic species of the open Black Sea during 1980-1995 and possible teleconnections // Besiktepe ST, Unluata U, Bologa AS (eds) Environmental degradation of the Black Sea: challenges and remedies. – Kluwer, Dordrecht, Netherlands, 1999. – P. 147-173.
30. *Ovchinnikov I. M., Popov Y.* Cold intermediate layer formation in the Black Sea // Oceanology. – 1987. – 2**7**, №5. – P. 739-748 (in Russian).
31. *Ozsoy E.* Sensitivity to global change in temperate Euro-Asian seas (the Mediterranean, Black Sea and Caspian Sea) // Malanotte-Rizolli P, Eremeev VN (eds) The eastern Mediterranean as a laboratory basin for the assessment of contrasting ecosystems. – Kluwer, Dordrecht, Netherlands, 1999. – P. 281-300.
32. *Prodanov K., Mikhaylov K., Daskalov G., Maxim K., Ozdamar E., Shlyakhov V., Chashchin A., Arkhipov A.* Environmental management of fish resources in the Black Sea and their rational exploitation // Studies and Reviews. – GFCM. 68, FAO, Rome. – 1997. – 178 p.
33. *Research* characteristic features of distribution and state of the most important Black Sea commercial fish stocks. Develop short-term fishery forecasts // YugNIRO STL Funds. – Kerch: YugNIRO, 1991. – 129 p.
34. *Revina N. I.* Biological research of the Black Sea and its fishing resources. On provision of anchovy and horse mackerel larvae with feed in the Black Sea // Proc. AzCherNIRO. – Kerch, 1964. – **23.** – P. 105-114 (in Russian).
35. *Samyshev E. Z., Rubinshteyn I. G., Zolotarev P. G., Litvinenko N. M.* Changeability of the Black Sea benthos structure in conditions of anthropogenic impact // Anthropogenic impacts on coastal ecosystems. – M., VNIRO. – 1986. – P. 52-71. (in Russian).
36. *Shiganova T. A.* Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure // Fish Oceanogr. – 1998. – **7**. – P. 305-308 (in Russian).
37. *Shlyakhov V. A., Chashchin A. K., Korkosh N. I.* Intensity of fisheries and dynamics of the Black Sea anchovy stocks // Biological resources of the Black Sea. – 1990. – P. 93-102 (in Russian).
38. *Shlyakhov V. A., Charova I. V.* Scientific data on the state of the fisheries resources of Ukraine in the Black Sea in 1992-2005 // Black Sea Ecosystem 2005 and Beyond. – 1st Biannual Sci. Conf., Abstr., 8-10 May. – Istanbul, Turkey, 2005. – P. 131-134.
39. *Shulman, G. E., Nikol'skiy V. N., Yuneva T. V., Minyuk G. S* et al. Fat content in Black Sea sprat as an indicator of fish food supply and ecosystem condishion // Marine Ecology Progress Series. – 2005. – **293.** – P. 201-212. (in Russian).
40. *Shushkina E. A., Musaeva E. I.* Structure of the plankton communities in the epipelagic zone of the Black Sea // Oceanology. – 1990. – **30**, No 2. – P. 306-310 (in Russian).
41. *Shushkina E. A., Musaeva E. I.* The role of medusae in the energy of the Black Sea plankton communities

// Oceanology. – 1983. – **23**. – P. 125-130 (in Russian).
42. *Shushkina E. A., Vinogradov M. E.* Fluctuations of the pelagic communities in the open regions of the Black Sea and changes influenced by ctenophore *Mnemiopsis* // The variability of the Black Sea ecosystem: natural and anthropogenic factors. – Moscow, 1991. – P. 248-261 (in Russian).
43. *Shushkina E. A., Musaeva E. I., Anokhina L. L., Lukasheva T. A.* The Role of Gelatinous Macroplankton, Jellyfish Aurelia, and Ctenophores *Mnemiopsis* and *Beroe* in the Planktonic Communities of the Black Sea // Oceanology. – 2000. – **40**, No 6. – P. 809-816 (in Russian).
44. *Sorokin Yu.* Essay on ecological situation in the Black Sea. *In* GFCM. Report of the second technical consultation on stock assessment in the Black Sea, Ankara, Turkey, 15-19 February 1993. FAO Fisheries Report, No 495. – FAO, Rome. – 1994. – P. 63-77.
45. *Sorokin Yu.* Essay on ecological situation in the Black Sea. *In* GFCM. Report of the second technical consultation on stock assessment in the Black Sea, Ankara, Turkey, 15-19 February 1993. FAO Fisheries Report, No 495. – FAO, Rome. – 1994. – P. 63-77.
46. *Sorokin Yu*. The Black Sea, Ecology and Oceanography.–Leiden: Backhyns Publ., 2002.–875 p.
47. *Tsikhon-Lukonina E. A., Reznichenko O. G.* Specific features in the diet of the ctenophore Mnemiopsis individuals of different size in the Black Sea // Oceanology. – 1991. – **31**, No. 3. – P. 442-443 (in Russian).
48. *Tsikhon-Lukonina E. A., Reznichenko O. G., Lukasheva T. A.* Quantitative regularities in the diet of the Black Sea ctenophore *Mnemiopsis leidyi* // Oceanology. – 1991. – **31**, No 2. – P. 272-276 (in Russian).
49. *Tsikhon-Lukonina E. A., Reznichenko O. G., Lukasheva T. A.* What does ctenophore Mnemiopsis feed in the Black Sea coastal waters on? // Oceanology. – 1992. – **32**, No 4. – P. 724-729 (in Russian).
50. *Vinogradov M. E., Shushkina E. A., Musaeva E. I., Sorokin P. Yu.* Ctenophore *M. leidyi* (A. Agassis) (Ctenophora: Lobat) – new settlers in the Black Sea // Oceanology. – 1989. – **29**, No 2. – P. 220-224 (in Russian).
51. *Vinogradov M. E., Sapozhnikov V. V., Shushkina E. A.* Ecosystem of the Black Sea. – Moscow, 1992. – 110 p. (in Russian).
52. *Vinogradov M. E., Shushkina E. A.* Temporal changes in zoocene structure in the Black Sea open areas // Oceanology. – 1992. – **32**, No 4. – P. 85-91 (in Russian).
53. *Vinogradov M. E., Shushkina E. A., Nikolaeva G. G.* State of zoocenoses in the open areas of the Black Sea in late summer 1992 // Oceanology. – 1993. – **33**, No 3. – P. 382-387 (in Russian).
54. *Zaitsev Yu.* Impact of eutrophication on the Black Sea fauna // Studies and Reviews. GFCM. 64. – Roma: FAO, 1994. – P. 63-86.
55. *Zaitsev Yu., Mamaev V.* 1997. Marine biological diversity in the Black Sea // A study of change and decline. – 1997. – P. 45-54.

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Вплив желетілого зоопланктону на запаси промислових риб та на їх промисел у Чорному морі: аналіз багаторічних рядів біологічних спостережень. О. Гришин, Г. Даскалов, В. Шляхов, В. Міхнева. Наведено наукова інформація про екосистему Чорного моря, відносна до взаємодії між желетілим планктоном та рибальством, проаналізовані багаторічні часові ряди спостережень головних компонентів пелагічного суспільства: риб та безхребетних, їх тренди и зв'язки між ними. Підсумкова інформація та результати аналізу будуть застосовані для формулювання гіпотез о зв'язках між желетілим планктоном (реброплави мнеміопсис, бероє, плеуробрахія, медузи) та іншими пелагічними популяціями та їх впливом на запаси риб. Результати цієї роботи можуть бути застосовані як фонове дослідження для наступних стадій проекту «EUROGEL»: експериментальних робіт, аналізу даних и моделювання.
Ключові слова: желетіли, реброплав мнеміопсис, зоопланктон, хамса, шпрот, ставрида, реброплав бероє, інтродукція, часові ряди, Чорне море

Влияние желетелого зоопланктона на запасы промысловых рыб и их промысел в Чёрном море: анализ многолетних рядов биологических наблюдений. А. Гришин, Г. Даскалов, В. Шляхов, В. Михнева. Дана научная информация об экосистеме Черного моря, относящаяся к взаимодействию между желетелым планктоном и рыболовством, проанализированы многолетние ряды наблюдений главных компонентов пелагического сообщества: рыб и беспозвоночных, обсуждены их тренды и связи между ними. Итоговая информация и результаты анализа будут использованы для формулирования гипотез о связях между желетелым планктоном и другими пелагическими популяциями и их воздействием на запасы рыб. Эта статья может быть использована как фоновое исследование для последующих стадий проекта «EUROGEL»: экспериментальных работ, анализа данных и моделирования.
Ключевые слова: желетелые, гребневик мнемиопсис, зоопланктон, хамса, шпрот, ставрида, гребневик берое, интродукция, временные ряды, Черное море