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ADDRESSING THE ECOLOGICAL ISSUE OF THE INVASIVE SPECIES

SPECIAL FOCUS ON THE CTENOPHORE *MNEMIOPSIS LEIDYI* (AGASSIZ, 1865) IN THE BLACK SEA

LYUDMILA KAMBURSKA, WOLFRAM SCHRIMPF, SAMUEL DJAVIDNIA

AND

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Institute for Environment and Sustainability

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EXECUTIVE SUMMARY

The report aims to address the ecological issue of the invasive species. The human-mediated invasions, often referred to 'biological pollution' are a worldwide problem that is increasing in frequency and magnitude, causing significant damage to the environment, economy and human health. *Bioinvasions* have strong impact on biodiversity and ecosystem functioning and stability. They are ranked as the second most important threat to biodiversity (after habitat destructions) by the World Conservation Union. "Trends in invasive alien species" is recognized as indicator of marine biodiversity and ecosystem health assessment, proposed and included in the EU set of headline biodiversity indicators (SEBI-Streamlining European 2010 Biodiversity Indicators) and EEA core set of indicators.

'Numbers and cost of alien invasions' is one of the indicators for assessing progress towards the 2010 target (UNEP/CBD/SBSTTA/10/INF/17, 2005). More, 'Inventory of the occurrence, abundance and distribution of non-indigenous species presented in the region/sub-region' is proposed as biological element in the initiative of the EC, the Marine Strategy Directive (COM, 2005). Some policy gaps remain in the area of prevention and control of invasive alien species. For this purpose, a key objective is to develop specific actions, including an early warning system.

A case study presented is an assessment of distributional mode, long-term dynamics and trends of the invasive ctenophore *Mnemiopsis leidyi* (Agassiz, 1865) in the Black Sea. This species has led to tremendous ecosystem changes and substantial economic losses in the late 1980s-1990s and it has been recognized as a problem of main ecological concern for the sustainable development of the region, together with the high level of anthropogenic forcing on the Black Sea ecosystem. Data from three Black Sea regions are combined, summarized and recent information on *M. leidyi* population distribution and occurrence, mesozooplankton pattern and the differences in between the regions is provided.

This report gives practical information to struggle with analogous invasions in other European Seas, using the example of the Black Sea. It could contribute to the debate on the development of EU headline biodiversity operational indicators in achieving the EU target of halting the loss of biodiversity by 2010.

1. INTRODUCTION

By definition "alien species" are non-native species, including its seeds, eggs, spores or other biological material capable of propagating that species, introduced deliberately or unintentionally outside their natural geographical range where they become established, proliferate and spread. "Invasive species" are aliens or non-indigenous species (NIS) whose establishments threaten ecosystems, habitats or species with economic or environmental harm (Article 8(h), CBD, 1992). Over the last few years the problem of biological invasions all over the world has been accelerated (Cohen, Carlton, 1998). Invasive species are acknowledged as one of the most significant threats to biodiversity through competition with native species, predation and disease transfer, together with habitat loss and fragmentation. The main vectors responsible for the transfer of marine organisms are ship's hulls and ballast waters, suggesting that ignoring the problem with ballast water introductions is analogous to playing ecological roulette (Cohen, Carlton, 1998; Moncheva, Kamburska, 2002). Recently, the initiatives have being undertaken by International Maritime Organization (IMO) regarding water ballast management and preventive measure against "illegal" migrants. The initiatives of the EU are targeting specific actions relating to invasive species, which are: (i) to update the list of invasive alien species (IAS) that are known to pose an ecological threat to native flora and fauna, habitats and ecosystems within the EU under the CITES Regulation; (ii) to include the list in the European Community Clearing House Mechanism (ECCHM) under the CBD; (iii) to facilitate the exchange of information, through the ECCHM, regarding existing legislation, guidelines and experience, including on measures taken to prevent the introduction, control or eradication of those alien invasive species; (iv) to continue promoting the elaboration of international guidelines to be adopted by the Parties to the CBD.

Among the enclosed seas, the Black Sea is recognized as a unique marine environment and one of the most environmentally degraded (Mee, 1992). With a permanent anoxia within 87 % of its volume, it is the largest anoxic basin of the World Ocean. Its surface area is five times smaller than its catchment basin. The environmental catastrophe in the Black Sea resulting from anthropogenic forcing, concomitant with natural variability and climatic changes, is manifested by dramatic ecosystem changes. Key factors of "highest concern" in contributing to deterioration of the basin are eutrophication and overexploitation of living resources (Stanners, Boudreau, 1995; Zaitzev, Mamaev, 1997). But the huge

number of the invasive species and their harmful impact emerged to a key ecological problem for the region too.

"Cumulative numbers of alien species in Europe since 1900" is a robust indicator showing the growing number of alien species established in Europe from 1900 onwards, using 10-year intervals, as proposed by the EEA. A historical trend adapted to the Black Sea invasive species is apparent (Fig. 1). The escalating number and variety of NIS especially in the late 1980s-1990s became an attribute of the Black Sea ecosystem as well (Moncheva, Kamburska, 2002). Among the other enclosed basins, Black Sea is ranked as highly invasive environment (Fig. 2). Accordingly to the plankton exotic index (a ratio of alien *vs*. indigenous species), it is twice higher during the period 1990-2002 in comparison to the period 1980-1990, which approximately means 1 new NIS documented each year.

The environmental impact caused by aliens is difficult to predict because of the uncertainties about their biological cycle in the novel environment and their interactions with the host biota. Some of them are appearing in extremely high concentrations, not recorded even in their native environments and causing hazardous environmental and socio-economic effects on the ecosystem health (Table 1).

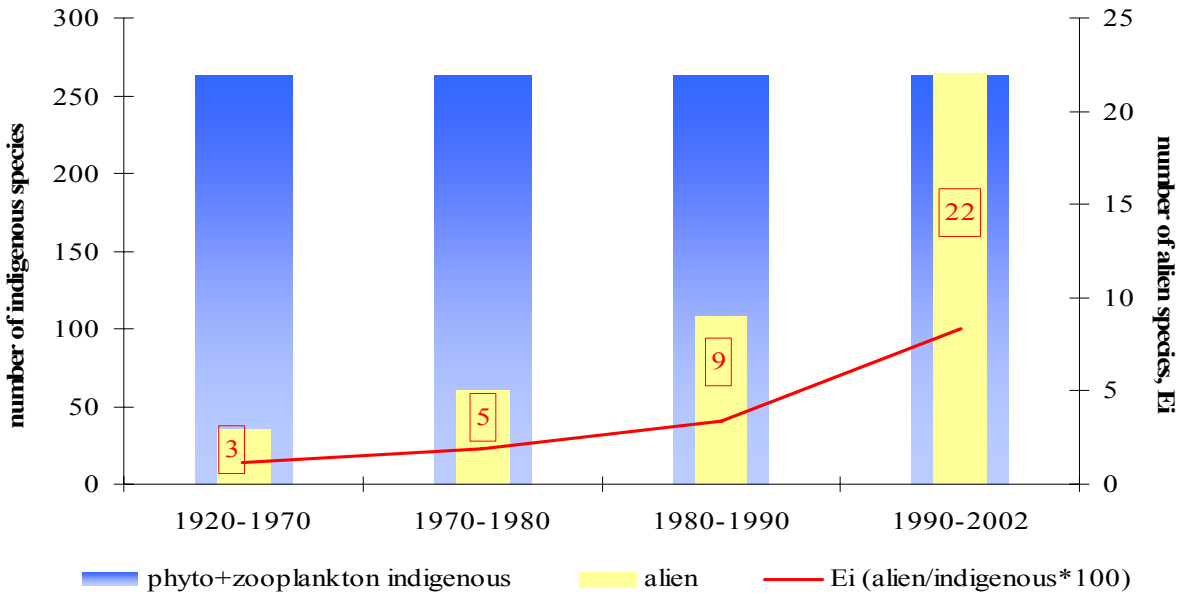


Figure 1. Number of indigenous and alien plankton species in the Western Black Sea (exotic index E*i* = aliens/indigenous species*100) (after Kamburska, Moncheva, 2003)

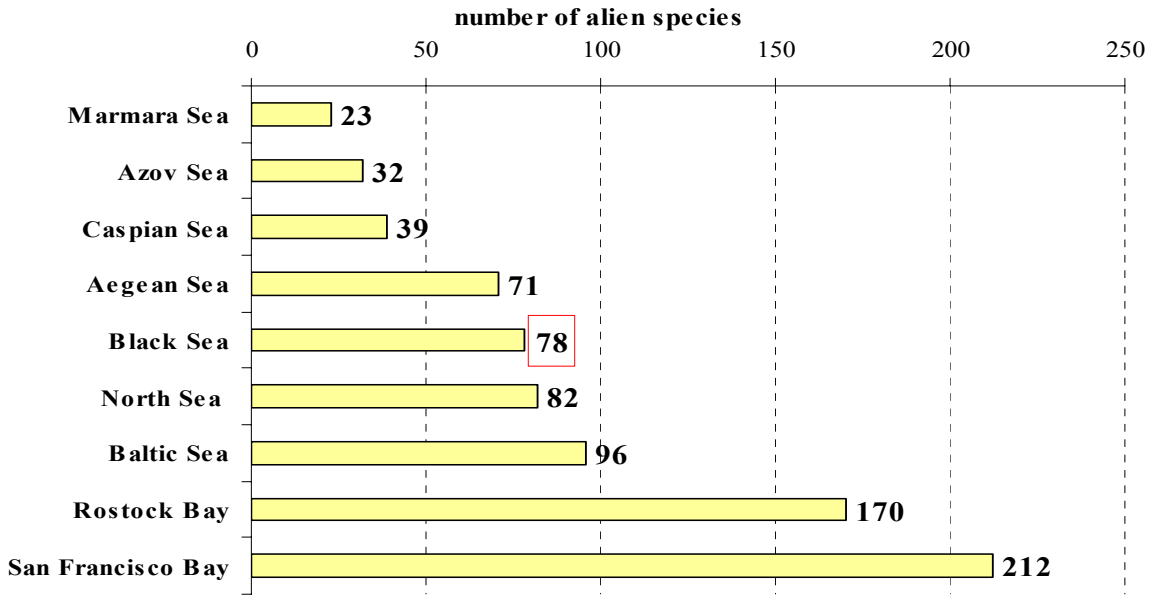


Figure 2. Number of alien species in different basins (Cohen, Carlton, 1998; Gollasch, Leppakoski, 1999; Zaitzev, Ozturk, 2001; Moncheva, Kamburska, 2002; Kamburska, Moncheva, 2003)

The increasing number of NIS could be perceived as an aspect of increased biodiversity (thus called xenodiversity), but it could be a reason for decreasing of native species diversity. Still under discussion is the question if the invasive species are a major cause of extinctions of natives (Gurevitch, Padilla, 2004). There are numerous examples of the ecological devastation caused by the introduction of non-indigenous species. An example of rapid spreading and undesirable impact on the ecosystem is the ctenophore *Mnemiopsis leidyi* (Agassiz, 1865) *(photo 1)* introduced to the Black and Azov Seas in the late 1980s. *M. leidyi* is listed as one of the 100 "World's Worst" invaders (Lowe et *al*., 2000). The species is a self-fertilizing hermaphrodite with a very high reproductive capacity (Kremer, Reeve, 1989) and its growth rate is comparable to that of phytoplankton, with daily doublings (Reeve et *al*., 1978). Naturally, such a high growth rate can only be supported with a very high feeding rate. Its "native" habitats are the Atlantic coastal waters of Northern and Southern America (Fig. 3), where it can be found in a wide range of environmental conditions. Species is tolerant to low dissolved oxygen (hypoxia conditions), temperature between 2°C and 32°C, and salinities from 2 to 39 ‰ (Purcell et *al*., 2001).

Table 1. Environment and socio-economic risk scale for the impact of invasive species: + -low; ++ -medium; +++ -high; ? –lack of data (after Moncheva, Kamburska, 2002)

Impact	**Global**	**Black Sea**
Environment		
alteration of taxonomic and functional groups of species	+++	+++
detrimental changes in the food web	+++	+++
changes in habitat	+++	+++
resources competition and limitation	+++	+++
introduction of potentially toxin producing species (harmful algal blooms, seaweeds)	+++	++
introduction of new disease agents or parasites	+++	+
genetic effects on native species (hybridization, change in gene pool, loss of native genotypes)	+++	+
extinction/ reduction of native population size	+++	+++
changes host/ parasite life cycle	++	+?
Socio-economic		
loss in commercial/ recreational species harvest	+++	+++
losses in aquaculture harvest	+++	+?
tourism	+++	+++
losses in shipping (clogging of pipes)	++	+
underwater constructions damage by fouling species	+++	++
increased costs for remediation	+++	+++
threat to underwater cultural heritage	++	+?
human health risk	+++	+?

In the early 1980s, the ctenophore was accidentally introduced by ballast waters from the Northern Atlantic into the Black Sea (Pereladov, 1988, Vinogradov et *al*., 1989) and subsequently it has spread into the Azov, Marmara, Mediterranean, and Caspian Seas (Shiganova et *al*, 2001*a*, 2001*b*, 2001*c*) (Fig. 3).

The history of *Mnemiopsis* invasion is well documented. There are several environmental factors promoting the introduction and species adaptation process. The Black Sea is highly eutrophicated, and it is recognized that disturbed or eutrophic environments facilitate the increase in gelatinous populations. Besides, *M. leidyi* adaptation was favoured by the lack of parasites, enemies and pathogens in the Black Sea. Moreover, the overfishing activity had diminished the potential and efficient competition of pelagic ichthyofauna and this was one of the main driving factors contributing to the *M. leidyi* outburst (Kamburska et *al*., 2003; Daskalov et *al*., 2005). Indeed, the effect of loss of fish diversity had facilitated the functioning of other trophic levels in the Black Sea food webs, which in this case was the jellyfish component. A niche was opened by the decline of some commercially important small pelagic fish and it was effectively filled by *M. leidyi* as “compensation”.

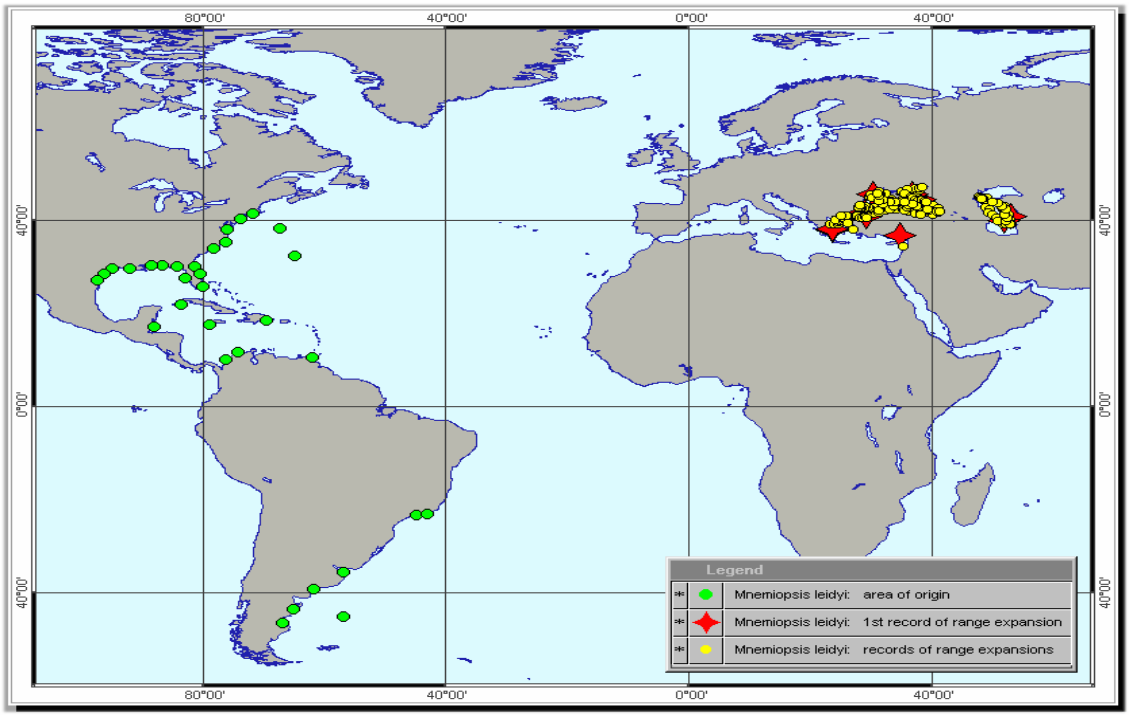


Figure 3. World wide distribution of *Mnemiopsis leidyi* (GAAS:www.zin.ru/projects/invasions/gaas) (●- area of origin; ●- range of expansion to novel environment, ◊- area of the 1st record)

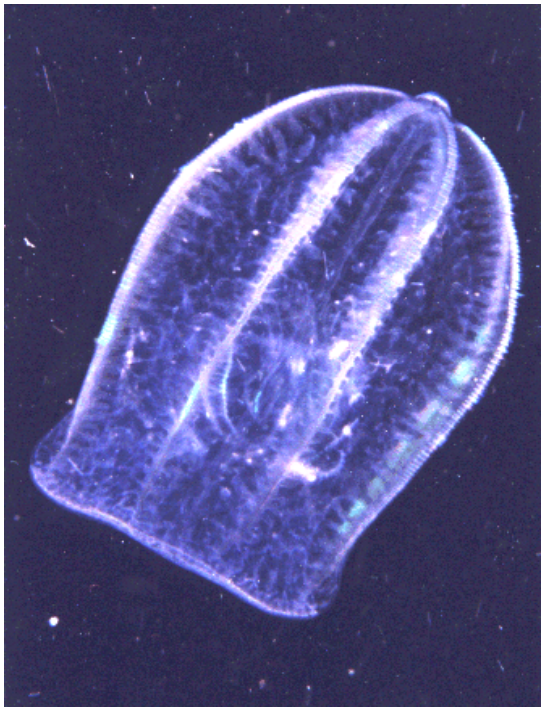
The ecological and physiological characteristics of this species comprise all "the right stuff" to produce harmful blooms (Kremer, 2001). The maximum density of *M. leidy*i which has been reported for the open Black Sea area is 4.6 kg wet weight per m^{-2} (7600 ind.m^{-2}) registered in summer/autumn 1988-1989 (Vinogradov et *al*., 1992). It was found in a concentration of 12 kg.m^{-2} off the Bulgarian coast in 1990 (Bogdanova, Konsulov, 1993). However, a substantial decrease from 1991 till 1993 was apparent, after which the trend was inverted again and *Mnemiopsis* was observed with maximum 9.7 kg wet weight per m^{-2} inshore in September 1994 (Shiganova, 1997). Although highest concentrations occur in summer (and early autumn), unlike in native regions, relatively high concentrations of *M. leidy*i were present during other seasons in the Black Sea as well (Kideys, Romanova, 2001). The spawning period is summer and coincides with the spawning season of anchovy in the Black Sea.

M. leidyi is a generalist, mainly feeds on pelagic crustaceans, but also ichthyoplankton and mussel veligers (Tzikhon-Lukanina, Reznischenko, 1991). This species is able to survive at very low prey density and to maintain its feeding rate proportional to prey concentration also (Kremer, 1979). The direct harmful effect of *Mnemiopsis*, especially in summer frequently provoked a critically low mesozooplankton stock (4.5 times less for copepods and 45 % decrease of

Cladocera biomass inshore), low diversity and hypoxia/anoxia at the bottom layer (due to mucus substances). Up to 70 % of total ichthyoplankton stocks in shallow waters were preyed by *Mnemiopsis*, together with 30 % decrease of zoobenthos due to the grazing on the benthic larvae. A remarkable decline of anchovy and sprat fisheries which used to have a turnover of about $200 mill./year in the 1980s was also recorded (Zaitzev, Mamaev, 1997). The eutrophic environment resulted in enhanced biological productivity which had guarantied the outburst of *M. leidyi* during the 1980s.

The Black Sea pelagic food-web has been conquered by *Mnemiopsis* albeit its large inter-annual and seasonal variability. The great modification of food web structure and functioning, and the trophic cascade effects led to a remarkable shift towards the pathway dominated by gelatinous in the pelagic food web (Finenko et *al*., 1995; Shiganova, 1997; Kamburska et *al*., 2003). *M. leidyi* became an "ecological engineer" species (Carpenter, Cottingham, 1997) and it has been nominated as a responsible for the coastal environment deterioration, fishery decline and speeding up eutrophication related processes (e.g. anoxia, caused by massive precipitation of mucus and dead ctenophores to the bottom (Mee, 1992; Volovik et *al*., 1993; Kideys, 1994; Shiganova, 1997). Hence, *Mnemiopsis* harmful impact was superimposed by the effects of eutrophication, overfishing and environmental deterioration (Kideys, 1994; Moncheva et *al*., 2001; Oguz, 2003). The crucial role of the climatic forcing on the Black Sea ecosystem productivity, shifts in phyto- and zooplankton associations, *Mnemiopsis* dynamics and commercial fish stocks have to be taken under consideration too (Niermann et *al*., 1999; Moncheva et *al*., 2001; Oguz, 2005).

Preventing future accidental introductions is almost impossible and future expansions of NIS in the Black Sea would not be surprising. Another ctenophore *Beroe ovata* sensu Mayer (1912) *(photo 2)* was reported for the first time in 1997 (Konsulov, Kamburska, 1998). Morphological and molecular evidence indicates that *B. ovata* belongs to a species that is different from the Mediterranean *Beroe ovata* sensu Chun (Bayha, et *al.*, 2004). The new species was introduced from the Northern Atlantic estuaries with ballast water (Konsulov, Kamburska, 1998; Seravin et *al*., 2002) and it is a specific predator of *M. leidyi* (Nelson, 1925; Swanberg, 1970).


(1)

(2)

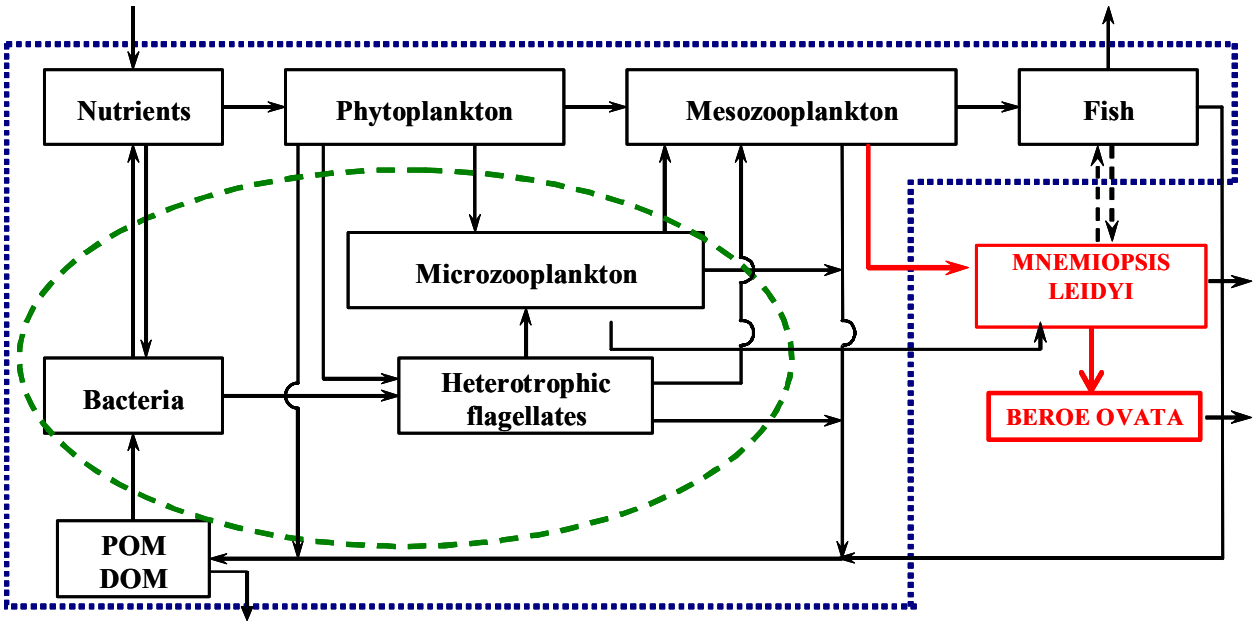
(1) Mnemiopsis leidyi (Agassiz, 1865); *(2) Beroe ovata* sensu Mayer (1912) / photos eng. Lyubomir Klissurov©, www.klissurov.dir.bg/

Depending on the anthropogenic pressures, the Black Sea ecosystem evolution has been subdivided in different phases (Moncheva et *al*., 2001; Kideys, 2002; Oguz, 2005). The 1960s-1970s symbolize thus called a "pristine" period. The late 1970s-1980s are recognized as a period of extremely nutrient loading in the basin and overfishing, while the 1990s-2000s are assumed to be predisposed to the climatic changes and reduction of the land-based nutrients load to the basin (Moncheva et *al*., 2001; Oguz, 2005). These ecological problems have provoked ecosystem alterations which have been well documented.

A specific feature of the Black Sea ecosystem is the frequent blooms of gelatinous species (Zaitzev, Mamaev, 1997). Based on "gelatinous species concept", the following periods were suggested: 1) a pristine period (considering the eutrophication), during which the medusa *Rhizostoma pulmo* prevailed (1960s-1970s); 2) a period of *Aurelia aurita* expansion, or pre-*Mnemiopsis* phase (1970-1980s); 3) a period recognized as "*Mnemiopsis* era" (late 1980-1990s) (Zaitzev, Mamaev, 1997; Oguz et *al*., 2001); 4) the recent period (after 1997), when a new ctenophore, *Beroe ovata* has been reported (Konsulov, Kamburska, 1998). After *Beroe* occurs in the Black Sea, it was expected to control effectively *Mnemiopsis* population, reducing the duration of its negative impact and contributing to the Black Sea ecosystem recovery by remodelling the food web (scheme 1).

The question why some pelagic ecosystems support large fish stocks whereas others are dominated by jellyfish has received much attention in marine ecology. It has been hypothesized that while fish forage most efficiently on large forms of zooplankton (Brooks and Dodson 1965), they may be out-competed by jellyfish if the prey stock is dominated by small size classes (Greve, Parsons 1977), and that fish recruitment can fail, due to prey depletion by large standing stocks of jellyfish (Möller, 1980). Another hypothesis is that the visibility regime may affect the distribution of tactile and visual predators such as jellyfish and fish (Eiane et *al.*, 1997). A theory has been worked out arguing that poor visibility in the water column may prevent the visually planktivorous fishes from obtaining the foraging rates required for population maintenance while tactile planktivores such as jellyfish, are not affected (Eiane et *al.*, 1997).

Phyto- and zooplankton (plankton) are key elements in the marine environment as they are essential for higher trophic levels productivity and are indicative of both natural and anthropogenic driven changes (Planque, Reid, 1998). Prey-predator interaction of both alien ctenophores is believed to be capable substantially to "remedy" the commercial fish stocks too (Shiganova et *al.*, 2000, 2001*d*, 2004; Kideys, 2002). Both ctenophores could be considered *keystone* species for the coastal Black Sea ecosystem, that have a great impact on the composition, structure, and functioning of the pelagic food web.



Scheme 1. Block-scheme of the Black Sea pelagic food web after the occurrence of *Beroe ovata* in 1997

However the uncertainties linked to a "successfully" interacting of the *M. leidyi -B. ovata* couple provokes many questions regarding the degree to which their trophic relationship may shape the Black Sea ecosystem. A flourishing of the medusa *Aurelia aurita* may be expected based on the competitive release of *M. leidyi* (Fraser, 1962). Moreover, *Beroe* has no enemy in the Black Sea which is in a favour of so-called "dead end" species. Blooms of alien ctenophores further add to the problem of gelatinous in the Black Sea and confronted the ecosystem with the "invasive complex" dilemma in which one invading species favours other invaders without any possibility to foresee the outcomes (GESAMP, 1997; Kamburska et *al*., 2003; Kamburska, 2004).

The objective in the present study is to analyze short and intermediate term trends of *M. leidyi* distribution faced to the predation by *B. ovata* after 1997, together with long term trends aimed at providing an insight into the those species variability in the Black Sea. The ecosystem functioning and stability are manipulated by *Mnemiopsis*, therefore indicators (measurements) for biodiversity and assessment of ecological health in respect to mesozooplankton were under discussion also.

2. MATERIALS AND METHODS

2.1. Study area

Independent data sets from three Black Sea regions were used to perform the study. Within the selected regions with varied trophic and hydrophysical conditions, gradients of the ecological status could be distinguished those depending on the temporal-spatial scale. The regions which had been investigated are (Fig. 4):

(i) *Region 1*: *North-Eastern Black Sea* (NEBS)- no enrichment of nutrients;

(ii) *Region 2*: *Western Black Sea* (WBS)- an area showing direct or indirect effects even if there is not always evidence of nutrient enrichment (Moncheva et *al*., 2002);

(iii) *Region 3*: *North-Western Black Sea* (NWBS)-a "problem area" regarding eutrophication, mainly to the Danube influence (Cociasu et *al*., 1997)

The regional classification- shelf area (< 200 m depths) and open sea or offshore (> 200 m depth) was used with a special focus on the variability of selected parameters (variables) at the sampling stations in the coastal waters.

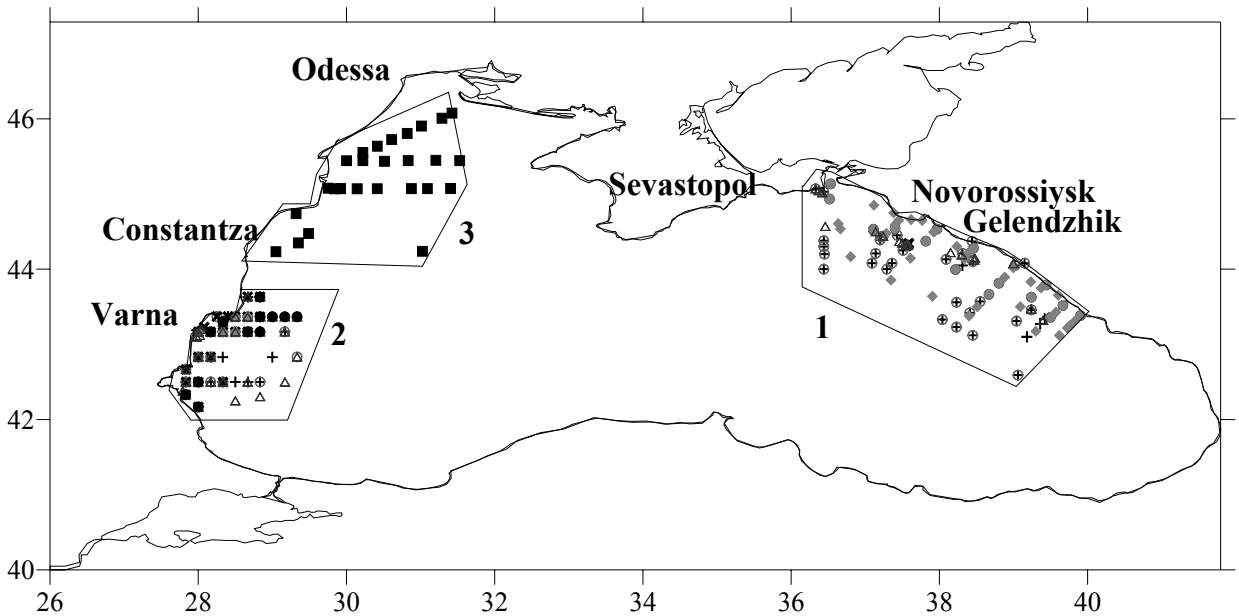


Figure 4. Map of sampling area during summers 1998-2004 (sampling stations + - 1998; ○ - 1999; Δ - 2000; ♦ - 2001; x - 2002; ● - 2003; ■ - 2004) by regions: 1 -North-Eastern, 2 -Western, 3 -North-Western Black Sea

2.2. Inventory of collected data and selected parameters

The summer period was chosen as a critical season for the pelagic ecosystem. The study is based on data obtained from samples collected from a number of monitoring stations at the shelf and offshore in various cruises during the summer period 1998-2004 (Tables 2, 3). Published data and long-term data of aliens and mesozooplankton community were used to reveal historical trends.

Chlorophyll *a* concentration values were extracted from 2-km gridded SeaWiFS product (Mélin et al., 2002, 2003) with average and standard deviation computed on squares of 3 x 3 grid points centred on the in situ measurement locations. The extraction has been performed for the daily, ten-days and monthly values associated with in situ measurement (data source IES, JRC).

Data sets include:

- *North-Eastern Black Sea* (Region 1) - temperature, salinity, mesozooplankton and jellyfish data obtained in cruises during 1998-2002 on station grid given in Fig. 4, Table 3;
- *Western Black Sea* (Region 2) - temperature, salinity, mesozooplankton and jellyfish data obtained in the frame of the multidisciplinary oceanographic investigations of IO-BAS, Varna, Bulgaria carried out during the period 1998-2004 on a standard network of stations (Table 3, Fig. 4);
- *North-Western Black Sea* (Region 3) - data for Jellyfish obtained during the POSEIDON cruise in September 2004 were provided by members of the scientific team (Niermann, Mihneva, 2004)

2.3. Methods

Field and laboratory methods

Temperature and salinity were obtained by the CTD "Sea Bird" system. The efforts for unification and intercalibration of applied sampling and laboratory methods for plankton between the Black Sea countries had been made through several regional and international projects (Niermann et *al*., 1995). Still the intercalibration is an ongoing process (Black Sea Zooplankton Manual, 2005), however the original data were obtained by comparable methodologies (sampling nets and depth layers). Zooplankton samples were collected with vertical hauls of Juday closing net (36-cm diameter) and filtrating gauze with a mesh size of 150 μm and 200 μm in the Western Black Sea, while the same type of net but with a mesh size of 180 μm in the coastal and 200 μm in open sea region of the North-

Eastern part was used. The hauls were taken from the layers: 0–thermocline, thermocline–pycnocline and pycnocline–anoxic layers in case of stratification. Samples were fixed to 4 % of formaldehyde. Quantitative analyses covered species abundance and biomass calculated per cubic or square meter. Individual standard weights and species length-weight relationships were used for calculation of the biomass (Petipa, 1959).

Jellyfish in the North-Eastern part were collected with a Bogorov-Rass net (with a 1 m^2 opening diameter, mesh size of 500 µm). A Hensen net (opening diameter 70 cm; mesh size 300 µm) was used in the North-Western part. Ctenophores were sorted and measured on board. Only data for the layer above the thermocline (the upper 20-35 m) were used at the stations due to the occurrence of *M. leidyi* in that layer. To find out the mode of *M. leidyi* distribution in time and space, abundance in ind.m^{-3} at each station was calculated. Morphometric parameters body length (L, mm), displacement volume (V, ml) and wet weight (WW, g) of each individual measured by using a laboratory balance were considered. Regarding the size structure of the population, three size classes were categorized to age groups based on the individuals body length (juveniles- up to 10 mm; transitional- 10-30 mm; adults- more than 30 mm length) (Mayer, 1912).

Statistical analyses

The statistical package Statistica 6.0 was used to distinguish zooplankton community characteristics in between the areas, regions and years and to recognize regularities and variances in the abundance distribution in time and space. Log-transformation of the data was necessary to homogenize the variance (Table 2).

Descriptive statistics, analysis of variance (ANOVA), Tukey test of honest significant difference of mean values of parameters (Tukey HSD), and principal component analyses (PCA), were applied to find out significant similarity/dissimilarity and to discriminate in between the regions and areas. The rotational strategy which has been used to obtain a clear pattern of loadings by PCA was a varimax rotation of the normalized factor loadings It aims at maximizing the variances of the squared normalized factor loadings across variables for each factor; which is equivalent to maximizing the variances in the columns of the matrix of the squared normalized factor loadings.

Table 2. Selected parameters and abbreviations

Parameter	*units*	*Abbreviation*
Temperature	[°C]	T
Salinity	[‰]	S
Chlorophyll *a* (SeaWiFS)	[mg.m^{-3}]	Chl *a*
mesozooplankton		mesozoo
total mesozooplankton abundance	[ind.m^{-3}]	zoo N
total mesozooplankton biomass	[mg.m^{-3}]	zoo B
Copepods, numerical abundance	[ind.m^{-3}]	*COP*
Cladocera, numerical abundance	[ind.m^{-3}]	*CLA*
Noctiluca scintillans, numerical abundance	[ind.m^{-3}]	*N. sci*
Jellyfish		
Mnemiopsis leidyi, numerical abundance	[ind.m^{-3}]	*M. leidyi*
Beroe ovata, numerical abundance	[ind.m^{-3}]	*B. ovata*

Table 3. Inventory of cruises, monitoring stations and data sources in the Black Sea (1998-2004)

region	**year, date**	**number of stations**		**parameter**	**research vessel, data source**
		shelf	**open sea**		
1-***NEBS***	1998, 29 Aug-05 Sept	13	24	T, S, mesozoo, jellyfish	R/V "Akvanavt", IO-RAS, Russia
	1999, 07-12 September	13	36	≡	R/V "Akvanavt", IO-RAS, Russia
	2000, 11-17 August	19	-	≡	R/V "Kvant"
	2001, 24 Aug-02 Sept	40	-	≡	Fishery vessel
	2002, 04-05 September	4	2	≡	R/V "Akvanavt", IO-RAS, Russia
2-***WBS***	1998, 23-26 September	19	5	T, S, mesozoo, jellyfish	N/V "Adm. Ormanov", NHS, Bulgaria
	1999, 20-24 September	21	4	≡	N/V "Adm. Ormanov", NHS, Bulgaria
	2000, 09-12 September	27	7	≡	R/V "Akademik", IO-BAS, Bulgaria
	2001, 19-23 August	10	-	≡	R/V "Akademik", IO-BAS, Bulgaria
	2002, 19-23 August	22	-	≡	R/V "Akademik", IO-BAS, Bulgaria
	2003, 09-13 September	11	2	≡	R/V "Akademik", IO-BAS, Bulgaria
	2004, 07-11 September	25	3	≡	R/V "Akademik", IO-BAS, Bulgaria
3-***NWBS***	2004, 1-6 September	27	-	jellyfish	POSEIDON cruise, (Niermann, Mihneva, 2004)
	Total number of stations	251	83		

3. RESULTS

3.1. *Mnemiopsis leidyi* distribution in the Black Sea during summer period 1998-2004

The obtained results for the distribution of the species reveal great variability in time and space. For the whole investigated period within the selected Black Sea regions, *Mnemiopsis* was found with the highest average abundance in the most eutrophicated region, the North-Western Black Sea (62 ± 192 ind.m^{-3}) (Table 4). Comparable values were recorded in the Western part (55 ± 80 ind.m^{-3}). On the contrary, the species sustained at a very low level in the North-Eastern Black Sea and it was exclusively rare (4 ± 7 ind.m^{-3}). The maximum value of *Mnemiopsis* was only 54 ind.m^{-3} in the NEBS, which was about 14 times lower than the peak registered in the NWBS and about 6 times lower than that one recorded in the Western Black Sea (326 ind.m^{-3}) (Table 4). Across the three regions, *M. leidyi* was found in a range of values up to 729 ind.m^{-3}.

In respect to the spreading of the ctenophore by areas, at the shelf stations (<200 m depth) and in the open sea waters (> 200 m depth), *Mnemiopsis* density was much higher in coastal waters compared to offshore areas. All the time it had significantly prevailed at the shelf stations in comparison to the deep sea (Table 5). During summer of the period 1998-2004, *M. leidyi* was narrowed to the surface waters in the layer above the thermocline (mostly at the shelf) where small copepods and cladocerans were more abundant (the forage zooplankton). The mean value of the species for the shelf area was 42± 91 ind.m^{-3}, while offshore it was only 5± 8 ind.m^{-3} (Table 5). The greatest quantity of *M. leidyi* by regions and areas was constantly registered at the shelf sampling stations in the North-Western and Western Black Sea (Table 6). The maximum of *Mnemiopsis* offshore was 52 ind.m^{-3}.

Pattern distribution of *Mnemiopsis* along the three regions by areas demonstrated a clear tendency– it was much more rarely found in the North-Eastern part (shelf and offshore). The species occurrence at the NEBS shelf was different from *Mnemiopsis* dispersal in the North-Western and Western Black Sea shelf, confirmed by the Tukey test of honest significant difference (HSD) at level $p < 0.05$ (Fig. 5). This could be related to the more frequently spread predator *B. ovata* in summer compared to the North-Western and Western Black Sea (Shiganova et *al*., 2004; Kamburska, 2004). The test does not demonstrate significant difference between the shelf and open sea area of Western and North-Western Black Sea (Fig. 5).

Table 4. Descriptive statistics of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}] in the Black Sea during summer 1998-2004 by regions (n- number of observations; NEBS: North-Eastern, WBS: Western, NWBS: North-Western Black Sea)

Region (n)	mean value	standard deviation	confidence - 95 %	confidence + 95 %	standard error	min. value	max. value	quartile 25 %	median	quartile 75 %
NEBS (151)	4	7	3	6	0.6	0	54	1	1	7
WBS (156)	55	80	43	67	6.4	0	326	2	16	81
NWBS (27)	62	192	-	138	36.9	0	729	2	4	16
all total (334)	33	81	24	42	4	0	729	1	4	19

Table 5. Descriptive statistics of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}] in the Black Sea during summer 1998-2004 by areas (shelf < 200 m, open sea > 200 m depth)

Area (n)	mean value	standard deviation	confidence - 95 %	confidence + 95 %	standard error	min. value	max. value	quartile 25 %	median	quartile 75 %
shelf (250)	42	91	30	53	5.8	0	729	1	6	36
open sea (84)	5	8	4	7	0.9	0	52	1	2	8
all total (334)	33	81	24	42	4	0	729	1	4	19

Table 6. Descriptive statistics of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}] by regions, areas (1998-2004)

Region, area (n)	mean value	standard deviation	confidence - 95 %	confidence + 95 %	standard error	min. value	max. value	quartile 25 %	median	quartile 75 %
NEBS shelf (89)	5	9	3	6	0.9	0	54	0.2	1	6
open sea (62)	4	5	3	6	0.6	0	19	0.6	2	8
WBS shelf (135)	62	83	48	76	7.1	0	326	3	18	90
open sea (21)	9	14	3	15	3	0	52	1	3	8
NWBS shelf (27)	62	192	-	138	36.9	0	729	2	4	16
all total (334)	33	81	24	42	4	0	729	1	4	19

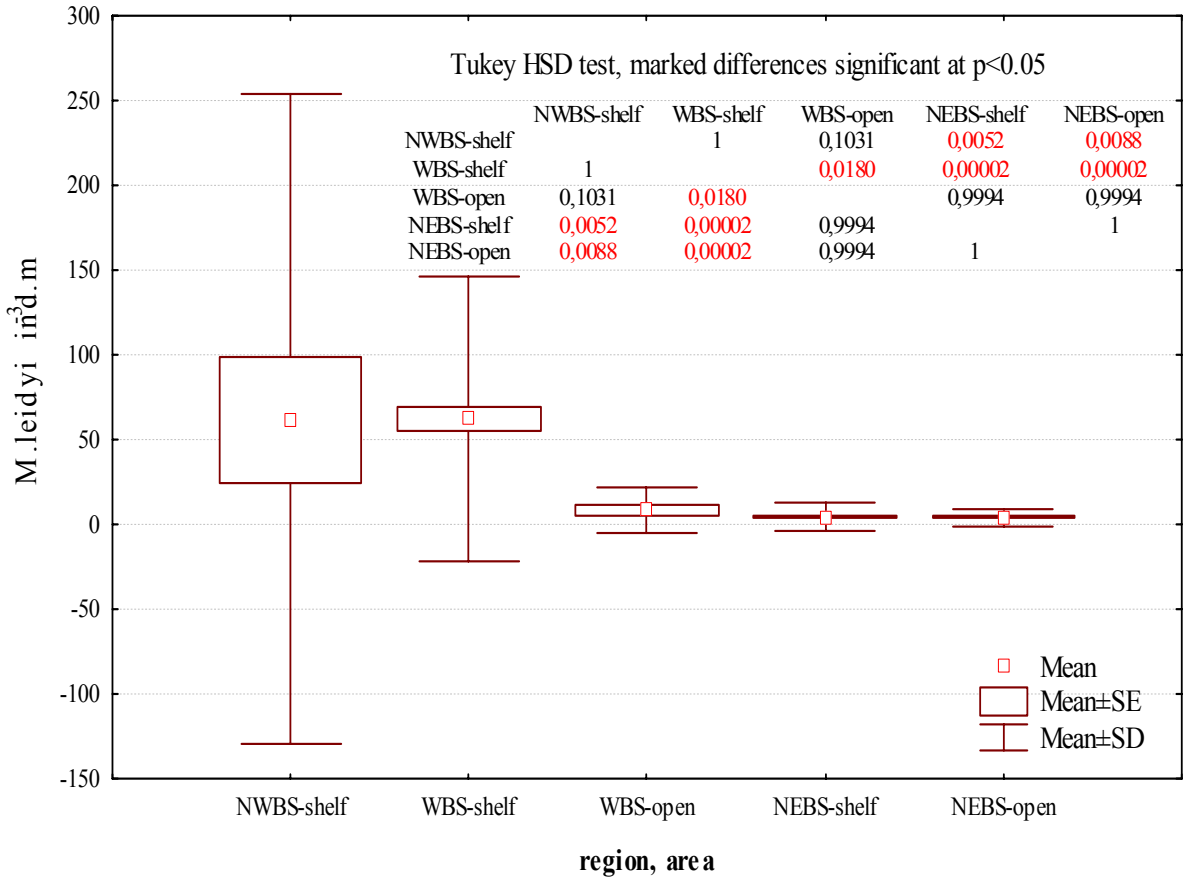


Figure 5. Box-Whisker plot of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}] by regions and areas in the Black Sea during summer 1998-2004 (NEBS-North-Eastern; WBS-Western; NWBS-North-Western Black Sea; n=334), Tukey test of honest significant difference of means (HSD)

For the first time data for *Mnemiopsis* density from the Western Black Sea are confronted with data from the North-Eastern part (Fig, 6, 7). Typical aspects of *M. leidyi* dynamics is significant intra- and interannual fluctuations, most probably related to the environmental interactions and food availability (Shiganova et *al.*, 2001*b*; Kamburska et *al.*, 2005). This characteristic was confirmed by our results too. A remarkable interannual variability in species distribution during summer of the period 1998-2004 was observed (Fig. 6-9). The ctenophore was rare in the North-Eastern Black Sea and it has reached the greatest value of 19 ind.m^{-3} (9± 4 ind.m^{-3}) during summer 1998 (Fig. 6). *Mnemiopsis* peak in the Western Black Sea was 292 ind.m^{-3} (66 ± 81 ind.m^{-3}) registered at transect Galata. Therefore some coastal areas in the WBS region could be considered as hot spots by reason of constantly retained high numbers of *Mnemiopsis* (bloom concentration). Such highly risked areas are the shallow stations at transects

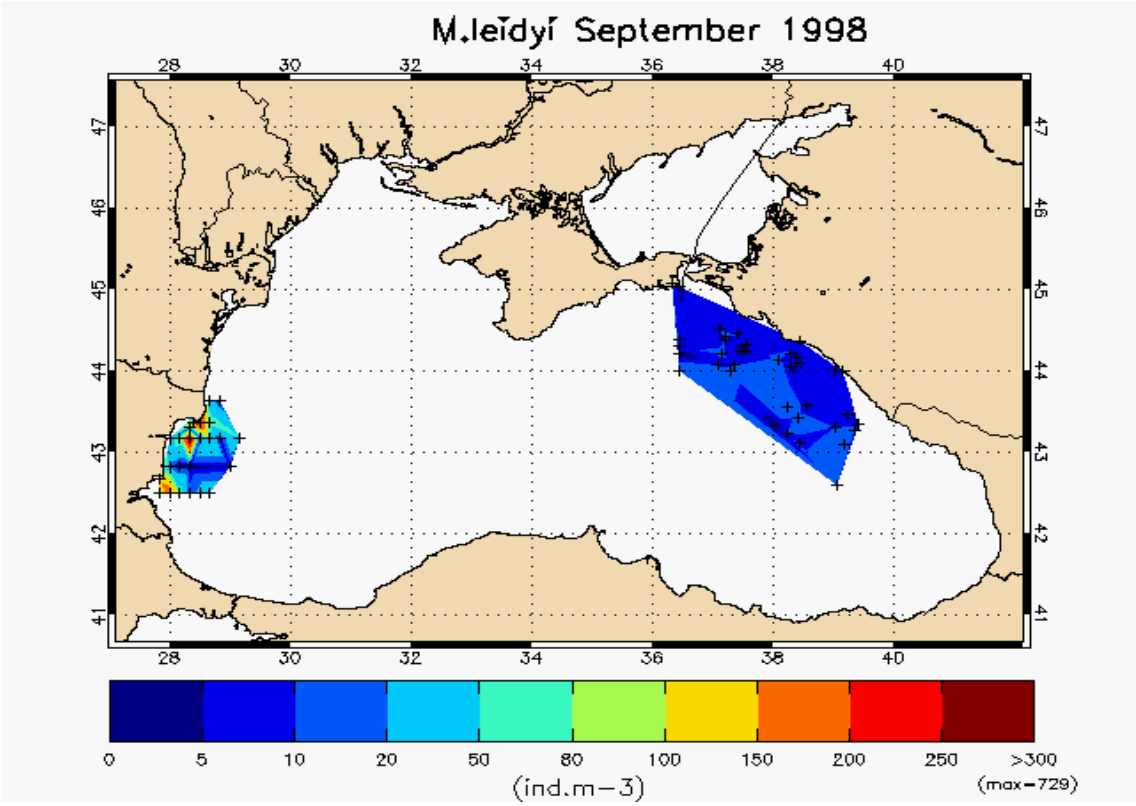
Kaliakra, Galata and Burgas in summer 1998 (Fig. 6). At that time the range of temperature was 18.91°C to 21.38°C, with an average of 20.34°C for the upper 10 meters layer.

During the investigated period, *M. leidyi* continually maintained a quite high concentration and frequency on the Western shelf with the exception of 1999 (Fig. 6). Indeed the density of species population in summer 1999 was abnormally low not only in the WBS, but in the whole Black Sea. Moreover, the ctenophore was completely missing in some areas in contrast to the previous and next years (Fig. 6). This was concomitant with increasing of mesozooplankton stock (Shiganova et *al.*, 2001*d*, 2004; Kamburska et *al.*, 2003). *Mnemiopsis* maximum in the North-Eastern Black Sea was barely 3 ind.m^{-3}. Even in the WBS region that year it has been constricted to maximum of 5 ind.m^{-3} on the shelf (Fig. 10). Most probably, its population was efficiently controlled by *Beroe ovata*, not ignoring the impact of other environmental factors. Moncheva et *al*. (2001) claimed the period 1997-1999 to be one of a decreasing trend in eutrophication (especially by phosphates and silicates) at higher temperatures.

Results from the studies indicate that the spatial distribution of the invasive species in summer 2000-2001 reveal higher density in the Western Black Sea compared to the North-Eastern part (Fig. 7). Species was more abundant compared to 1999, but sustained at a lower level than in summer 1998. The range of *Mnemiopsis* numerical abundance in summer 2000 in the Western Black Sea was to 243 ind.m^{-3}, while in summer 2001 it reached only 62 ind.m^{-3}. Species was rarely spread in the North-Eastern part in contrast to WBS (Fig. 7). It varied to 31 ind.m^{-3} in 2000 and to 54 ind.m^{-3} in 2001, all registered at the shelf station (Fig. 10).

Mnemiopsis was recorded in a huge amount in the Western Black Sea also in summer 2002 (Fig. 8). In average for the region it reached 156 ± 108 ind.m^{-3} with a maximum of 326 ind.m^{-3} registered at the shelf (Fig. 10). Similar to summer 1999, the numerical abundance of the ctenophore in the NEBS was very low in 2002 (maximum 3 ind.m^{-3}). Identical to 1999, *Mnemiopsis* was almost absent in summer 2003 in the Western Black Sea (Fig. 8).

The highest value of *Mnemiopsis* for the whole investigated period was recorded in the NWBS in 2004 at a coastal station, close to the Danube delta (Fig. 9).



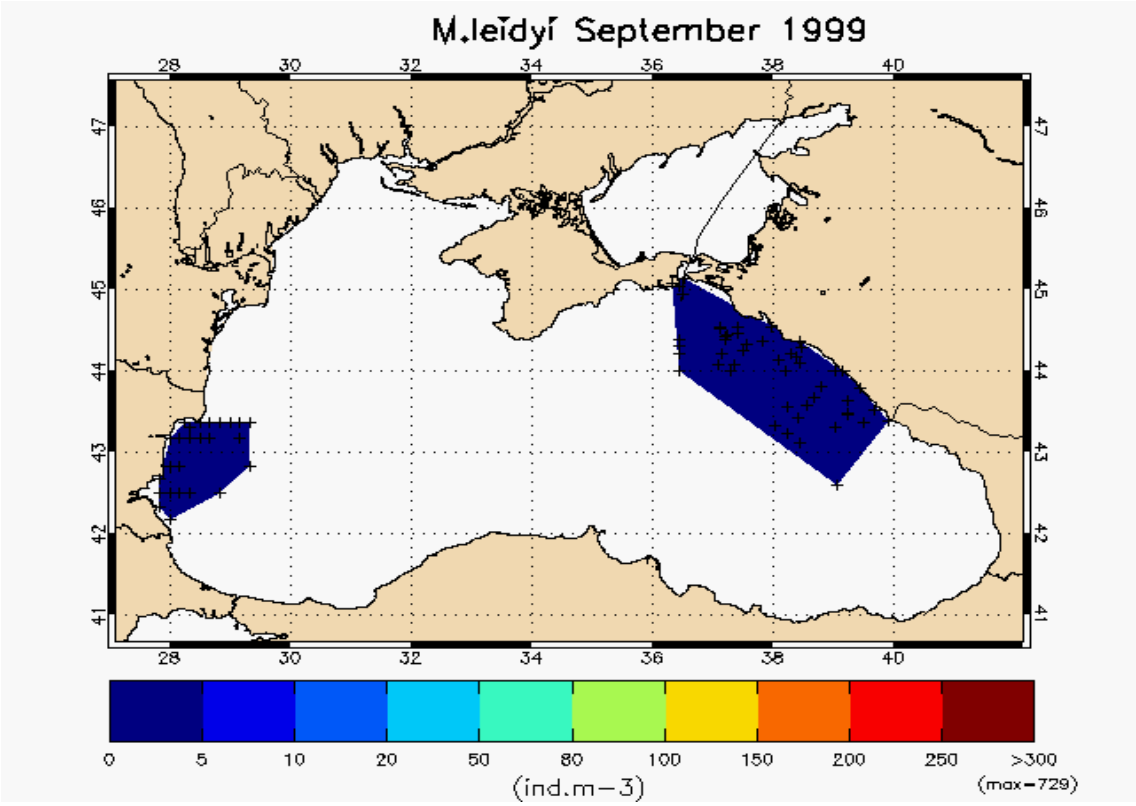
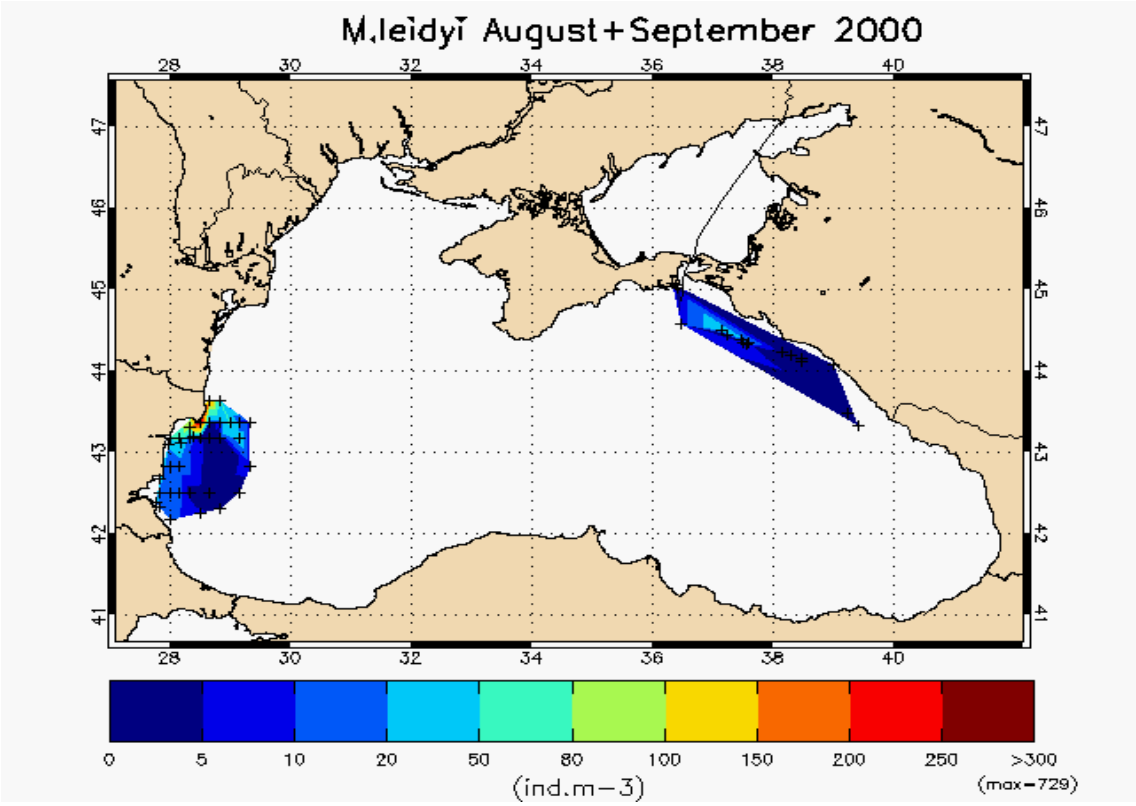


Figure 6. Spatial distribution of *Mnemiopsis leidyi* [in ind.m^{-3}] in the mixed layer above the thermocline during summer 1998-1999 (+ sampling station)



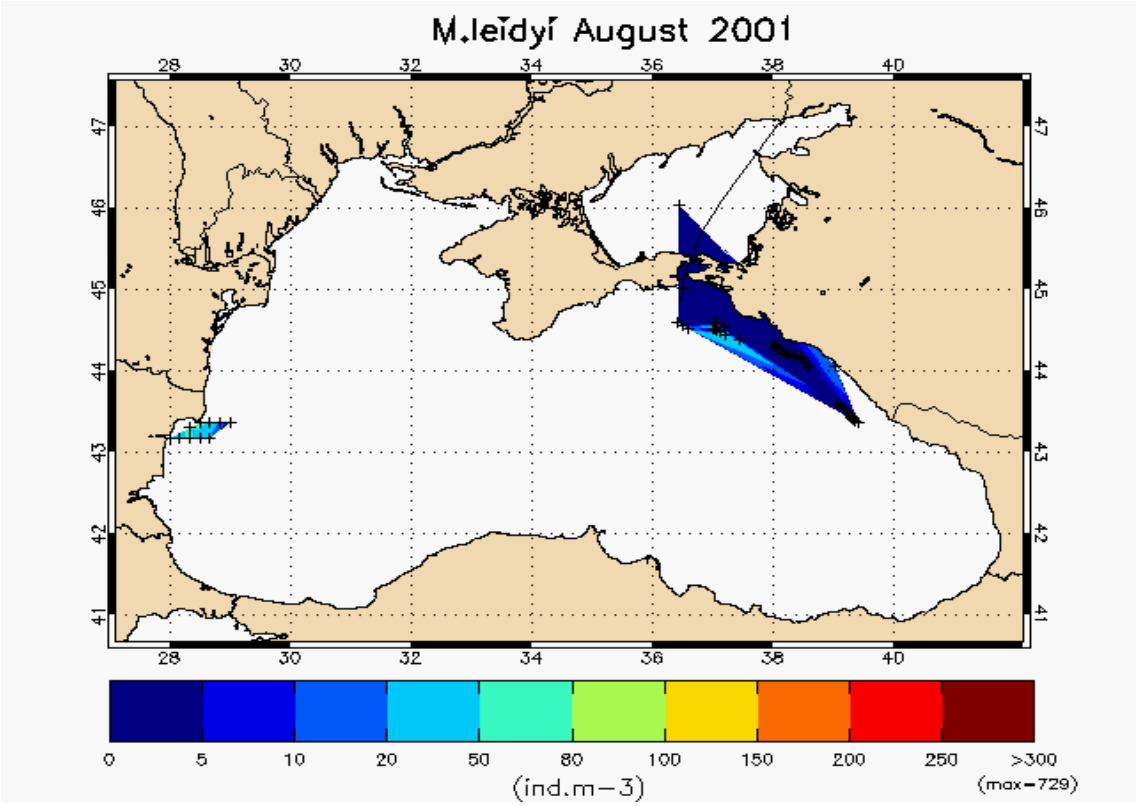


Figure 7. Spatial distribution of *Mnemiopsis leidyi* [in ind.m^{-3}] in the mixed layer above the thermocline during summer 2000-2001 (+ sampling station)

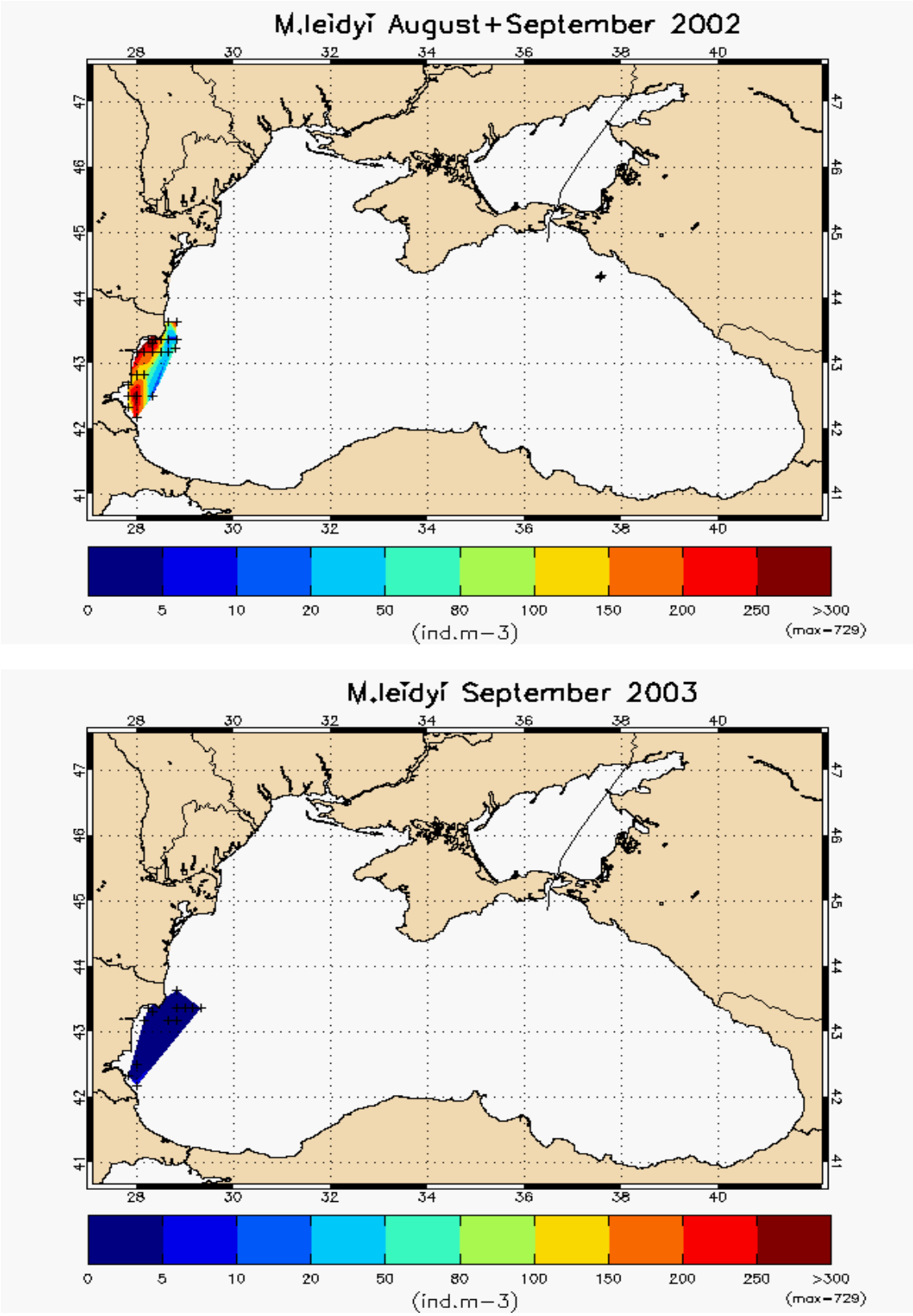


Figure 8. Spatial distribution of *Mnemiopsis leidyi* [in ind.m^{-3}] in the mixed layer above the thermocline during summer 2002-2003 (+ sampling station)

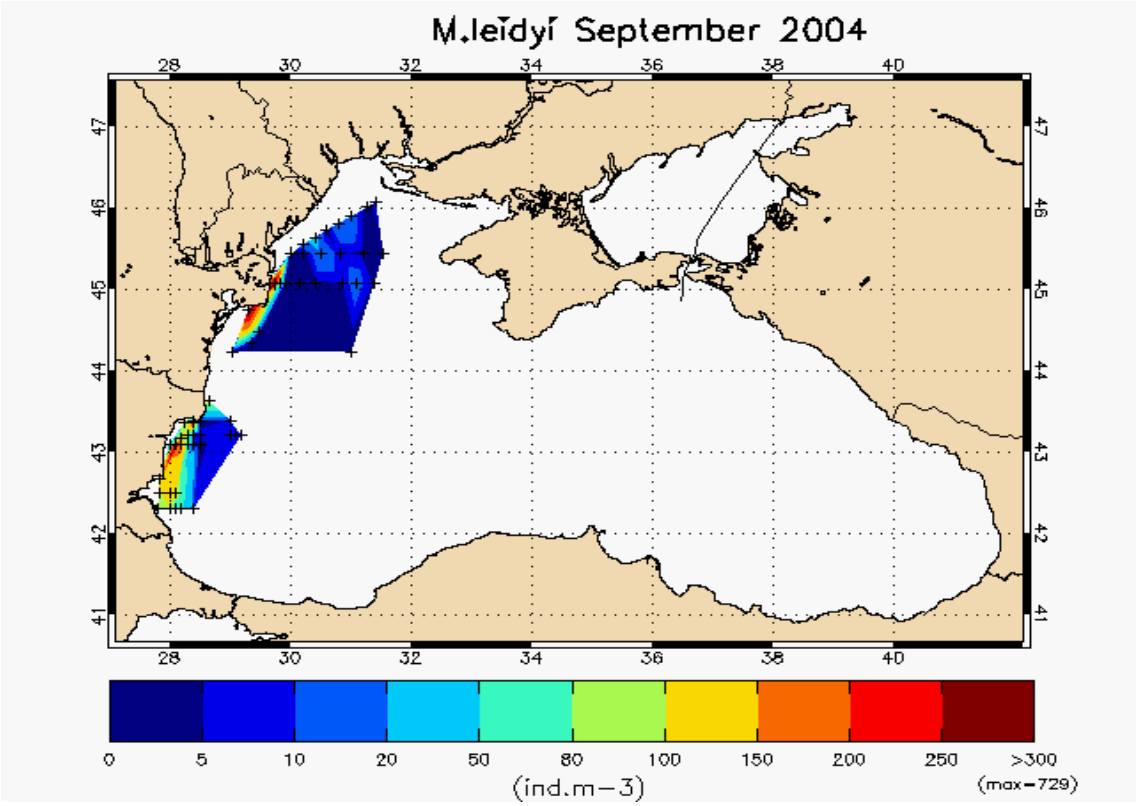


Figure 9. Spatial distribution of *Mnemiopsis leidyi* [in ind.m^{-3}] in the mixed layer above the thermocline during summer 2004 (+ sampling station)

The *Mnemiopsis* peak registered along the North-Western coast in 2004 (729 ind.m^{-3}) was three times higher compared to the maximum on the WBS shelf, whereas the average abundance of the species for both regions was comparable.

For the whole investigated period *M. leidyi* remained at a level of not more than 10 ind.m^{-3} in average for the whole North-Eastern Black Sea region. Most likely, this could be related to more frequently distributed predator *B. ovata* during summer contrary to the North-Western and Western Black Sea (Fig. 10).

During summer season of the period 1998-2004, *M. leidyi* sustained at a level much lower than the concentrations typical for the late 1980s (Shiganova, 1998). Even if it was rare in 1999 and 2003, it was found with relatively high densities in 2002 and again in 2004 in the Western and NW Black Sea (Fig. 11).

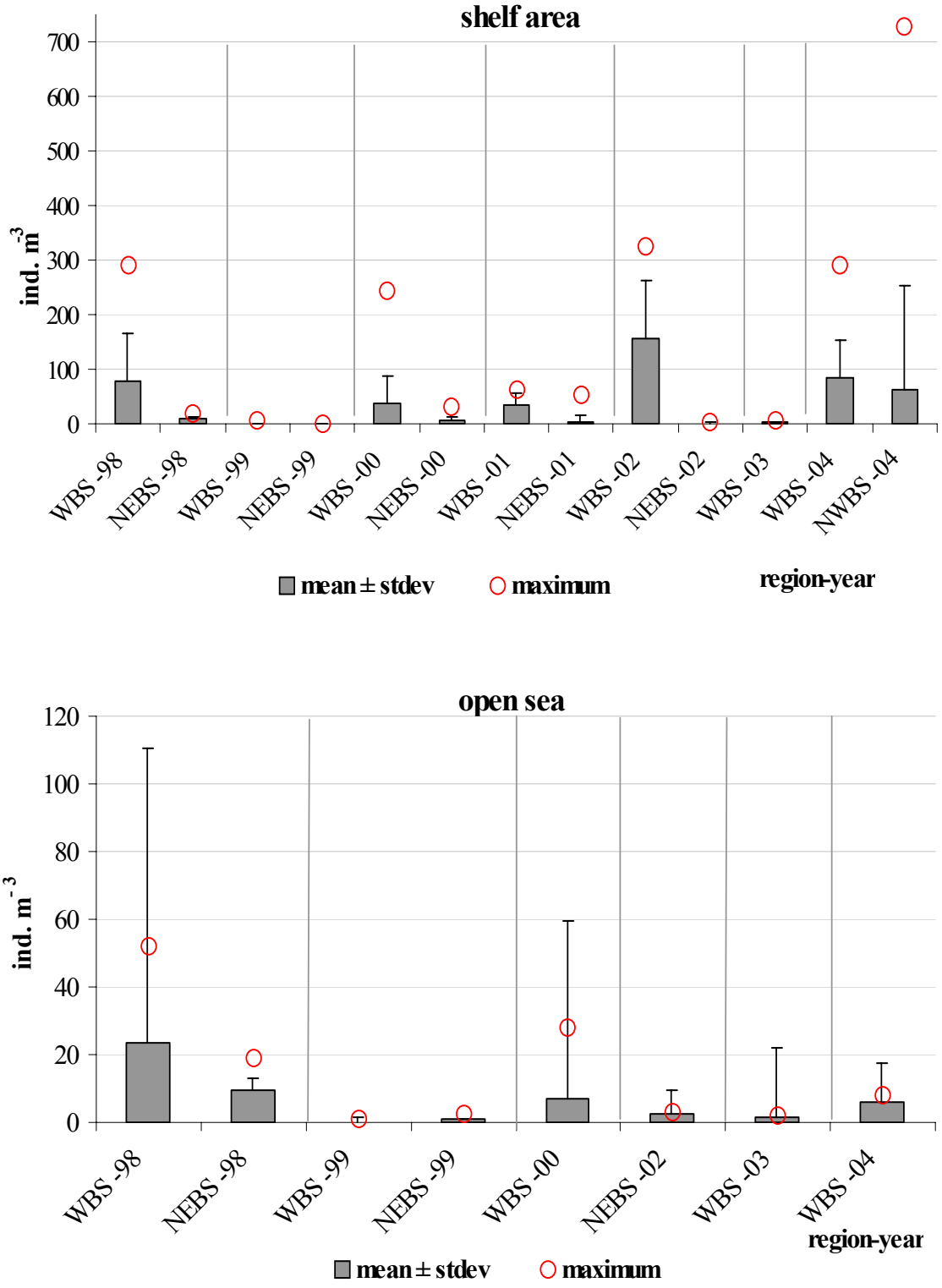


Figure 10. Interannual variability of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}] by regions (NEBS-North-Eastern; WBS-Western; NWBS-North-Western) and areas (shelf, open sea), summer 1998–2004

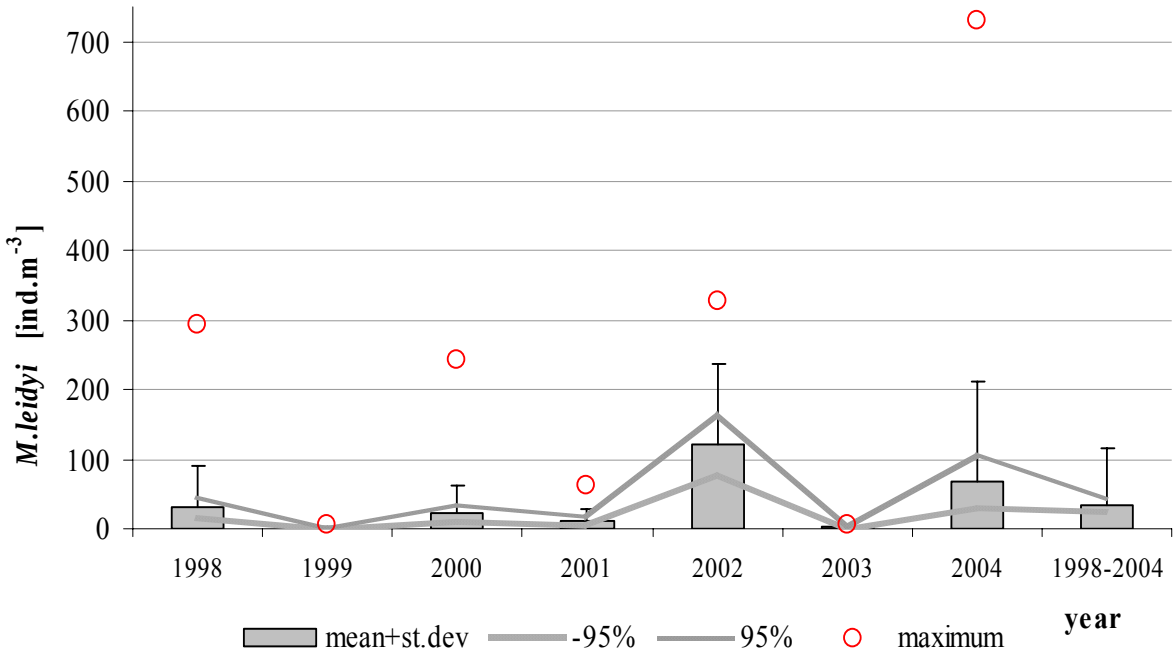


Figure 11. Interannual fluctuations of *Mnemiopsis leidyi* numerical abundance [ind.m^{-3}], summer season (n=334)

Because of the strong year-to-year fluctuations of the gelatinous plankton, individual years may be identified as "poor", "normal" or "rich" (Buecher, 2001). Taking into account that *Mnemiopsis* intense reproduction is the summer period (July-September) in the Black Sea, and also indicative of species dynamic for the whole year, we could apply the above classification for the period being discussed.

Mnemiopsis was rare or absent, with extremely low density not only offshore, but also at the shelf stations in 1999 and 2003 (Table 7, in yellow). The ctenophore kept mean values below 10 ind.m^{-3} (with maxima too). This abundance is used to qualify a bloom of medusa (Nival, Gorsky, 2001). So far as medusoid and ctenophore species have a similar ecological role, we apply the same *threshold* for considering *Mnemiopsis* as a rare and those years as "poor". Although *Mnemiopsis* maintained higher values in 2001 (as well maxima recorded), the Tukey test of HSD for unequal sample sizes ($p < 0.05$), does not demonstrate a difference of the means to the "poor" years, giving arguments to label 2001 also as a "poor" *Mnemiopsis* year.

As apparent from the data on *M. leidyi* density, the interval 1998-2004 can be classified as follows: "normal" years were 1998, 2000, 2002 and 2004, for the reason that the abundance of *M. leidyi* was maintained lower than the blooming concentrations typical for the late 1980s-middle 1990s (Vinogradov et *al*., 1989).

For instance the maximum in the Western part of 12 kg.m^{-2} was found in April 1990 (Bogdanova, Konsulov, 1993). Species abundance was quite high at the shelf stations for all "normal" years, whereas it decreased substantially offshore (Table 7). Indeed, the test of Tukey HSD confirms the differences between "normal" years, "poor" years and offshore area.

Mnemiopsis density was lower in the North Eastern Black Sea in contrast to NWBS and WBS, even during the summers of the "normal" years (Fig. 10). Even if the demographic structure of the species population was constituted by more than 90 % juveniles (an indicator of intensive reproduction) and its "physiological advantage" to emerge directly from larvae and gametes (Malashev, Archipov, 1992), subsequently *Mnemiopsis* was not plentiful and it had remained relatively low during those years (Table 7, in red). However, a bloom of *M. leidyi* was not observed during the summer period of 1998-2004. It seems *Mnemiopsis* presenting a cycle of high /low abundance or absence in the Black Sea, or in other words succession of poor–normal -rich years, the duration of which periods is irregular.

Table 7. Numerical abundance of *Mnemiopsis leidyi* [ind.m^{-3}] in the Black Sea during summer of the period 1998-2004 by areas (shelf and open sea) (descriptive statistics, n- number of observations)

area-year (n)	**mean ± std. dev**	**confidence**		**std. error**	**max. value**	**quartile 25 %**	**median**	**quartile 75 %**
		- 95 %	**+ 95 %**					
shelf-98 (32)	49 ± 75	22	76	13	**292**	7	12	65
shelf-99 (33)	1 ± 1	1	1	1	5	0	0	0.3
shelf-00 (46)	23 ± 43	11	36	6	**243**	3	9	23
shelf-01 (50)	11 ± 18	6	16	3	62	0	1	18
shelf-02 (26)	132 ± 114	86	178	22	**326**	7	112	229
shelf-03 (11)	2 ± 2	1	3	1	6	1	2	3
shelf-04 (52)	72 ± 145	32	113	20	**729**	4	15	94
open sea-98 (29)	12 ± 10	8	16	2	52	7	10	12
open sea-99 (41)	1 ± 1	1	1	0	3	1	1	1
open sea-00 (7)	7 ± 10		16	4	28	1	3	8
open sea-02 (2)	3 ± 1		9	1	3	2	3	3
open sea-03 (2)	2 ± 1		8	1	2	1	2	2
open sea-04 (3)	6 ± 2	1	11	1	8	4	6	8
all (334)	33 ± 81	24	42	4	729	1	4	19

3.2. *Mnemiopsis leidyi* in relation to some environmental factors

The spreading of *M .leidyi* along the regions certainly is related to the variability of the environmental parameters. Its dispersion and dynamics depend mainly on the temperature, salinity and food supply. *Mnemiopsis* has been reported as voracious predator on zooplankton (Burrell, Van Engel, 1976; Mountford, 1980). The most significant aspect of its feeding behaviour is that its ingestion rate is proportional to food concentration (Reeve et *al*., 1978). As a result, a great reduction in number and biomass of mainly copepods, other zooplankton groups, and fish eggs and larvae is often observed. Finenko, Romanova (2000) calculated that on a daily basis, about 20 % of total fodder zooplankton was being eaten by this ctenophore in the summer of 1995. Comparable values in the Black Sea were found by other scientists (Tsikhon-Lukanina, Reznichenko, 1991; Shiganova et *al*., 2001*b*) and also in the Caspian (Shiganova et *al*., 2001*a*, *c*; Kideys, Moghim, 2003; Finenko et *al*. 2005).

Regarding mesozooplankton total abundance, biomass and dominant taxonomic groups Copepods and Cladocera (key components of *Mnemiopsis* diet), the results revealed higher values in the North-Eastern Black Sea compared to the Western part (Fig. 12). Thus the mean zooplankton biomass on the Western shelf (63.24 ± 80 $mg.m^{-3}$) was roughly 5 times lower compared to the NEBS shelf and 2 times less than the registered in the NEBS open sea waters (Fig. 12). Similarly was the distribution of the total mesozooplankton abundance by regions. Besides, Cladocera group was the element discriminating among the regions. Its mean abundance reached to 7362 $ind.m^{-3}$ on the shelf in the NEBS (± 12184 $ind.m^{-3}$), while it was reduced at about 17 orders of magnitude to the Western part (Fig. 12). On the contrary, copepods manifested rather greater quantity in the WBS (maximum of 9537 $ind.m^{-3}$). The observed distributional pattern of lower mesozooplankton quantity in the WBS (particularly on the shelf), could be related to the widespread *Mnemiopsis leidyi* during that time in the area, while it sustained a very low density in the NEBS (shelf and open sea areas) (Fig. 12).

Although the opportunistic dinoflagellate *N. scintillans* (competitive to *M. leidyi*) maintained equal densities in both regions (Fig. 12), high concentrations (a bloom) during summer were recorded only at inshore stations in the Western part (about 7500 $ind.m^{-3}$).

Similar to the observed mode of spatial distribution of *Mnemiopsis leidyi*, the spreading of mesozooplankton along the investigated regions reveal significant interannual fluctuations (Fig. 13-15).

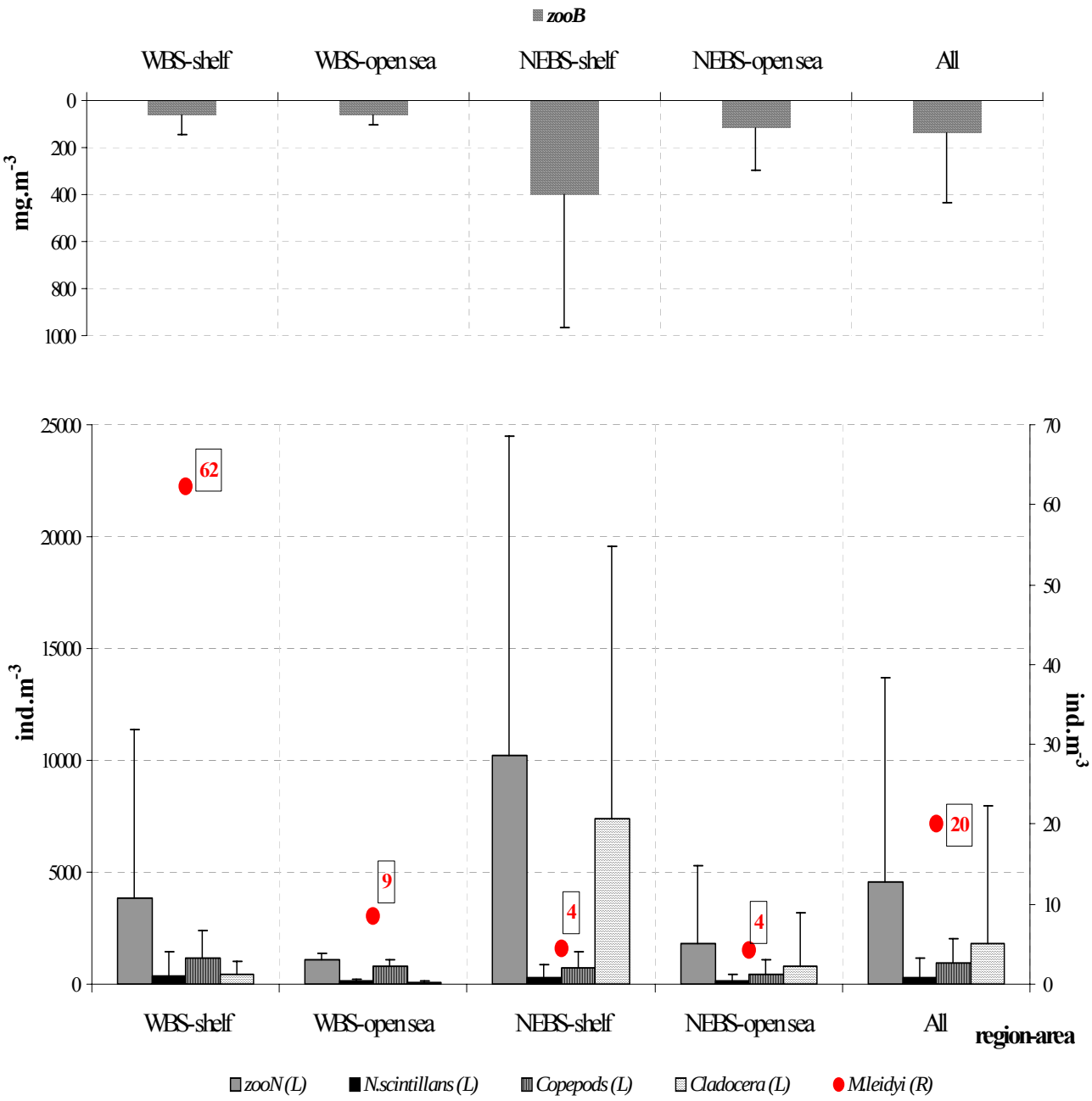
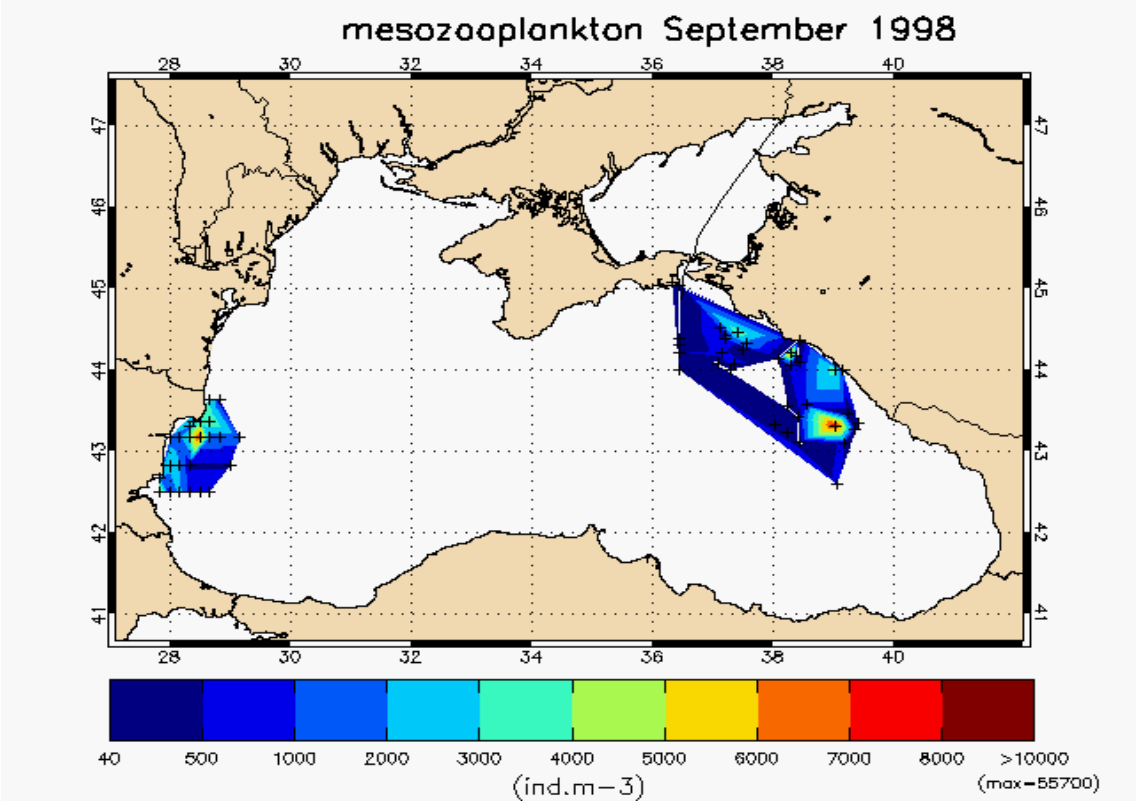


Figure 12. Mesozooplankton community characteristics in summer (1998-2004) by regions (WBS-Western, NEBS- North-Eastern) and areas (shelf, open sea). *Top panel*: zooB – mean mesozooplankton biomass [mg.m^{-3}] (n=170); *bottom panel*: zooN – mean mesozooplankton abundance, *N. scintillans*, Copepods, Cladocera [ind.m^{-3}] (left axis); *Mnemiopsis leidyi* mean abundance [ind.m^{-3}] (right axis) (n=307)



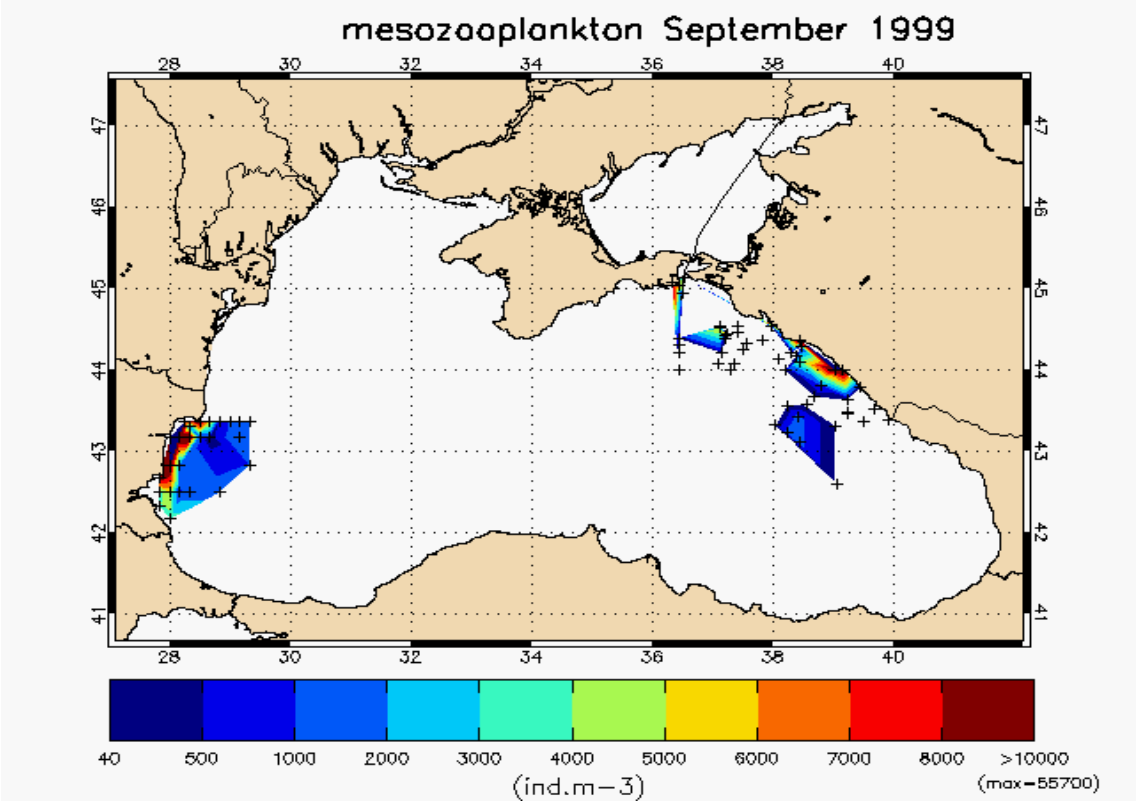
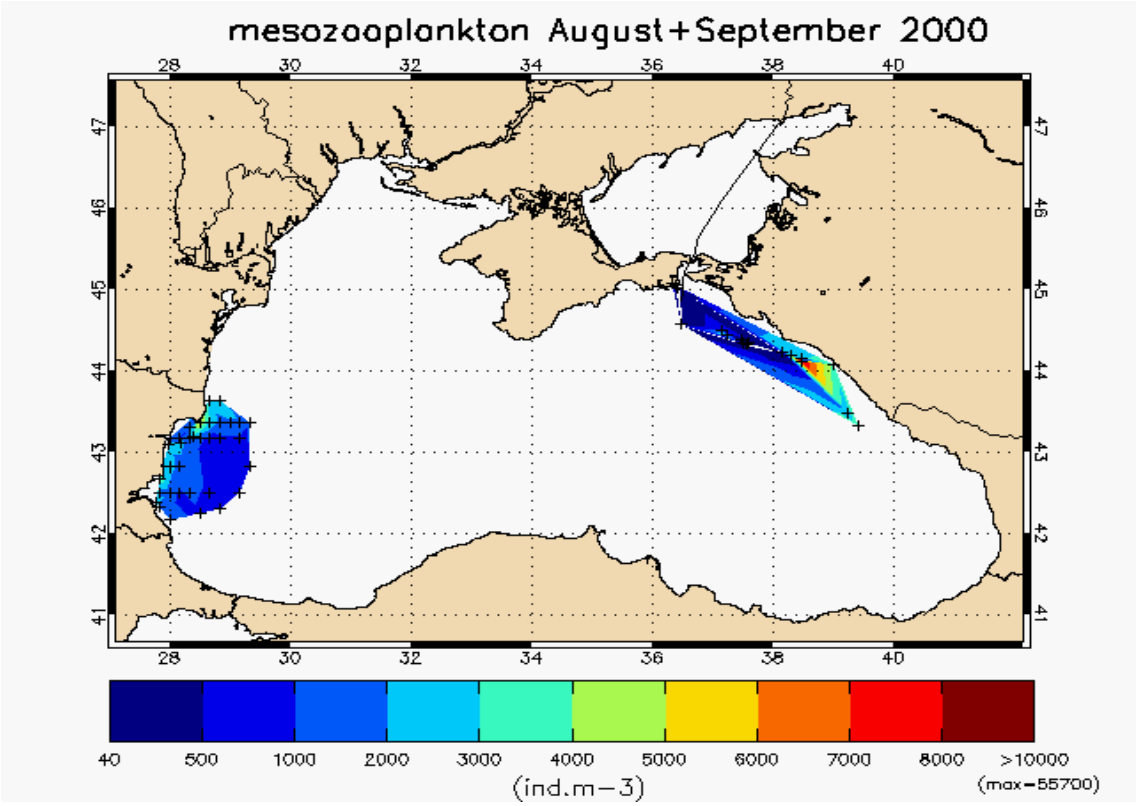


Figure 13. Total mesozooplankton numerical abundance [ind.m^{-3}] in the mixed layer above the thermocline during summer 1998-1999 (+ sampling station)



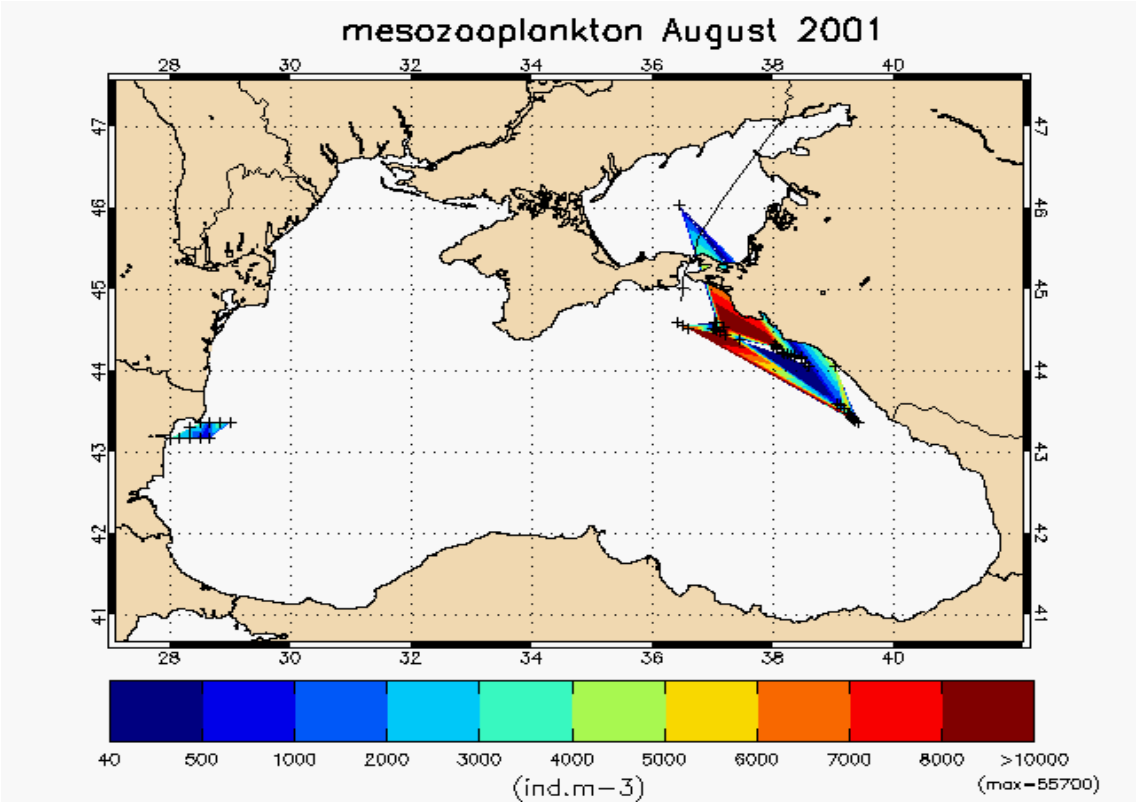


Figure 14. Total mesozooplankton numerical abundance [ind.m^{-3}] in the mixed layer above the thermocline during summer 2000-2001 (+ sampling station)

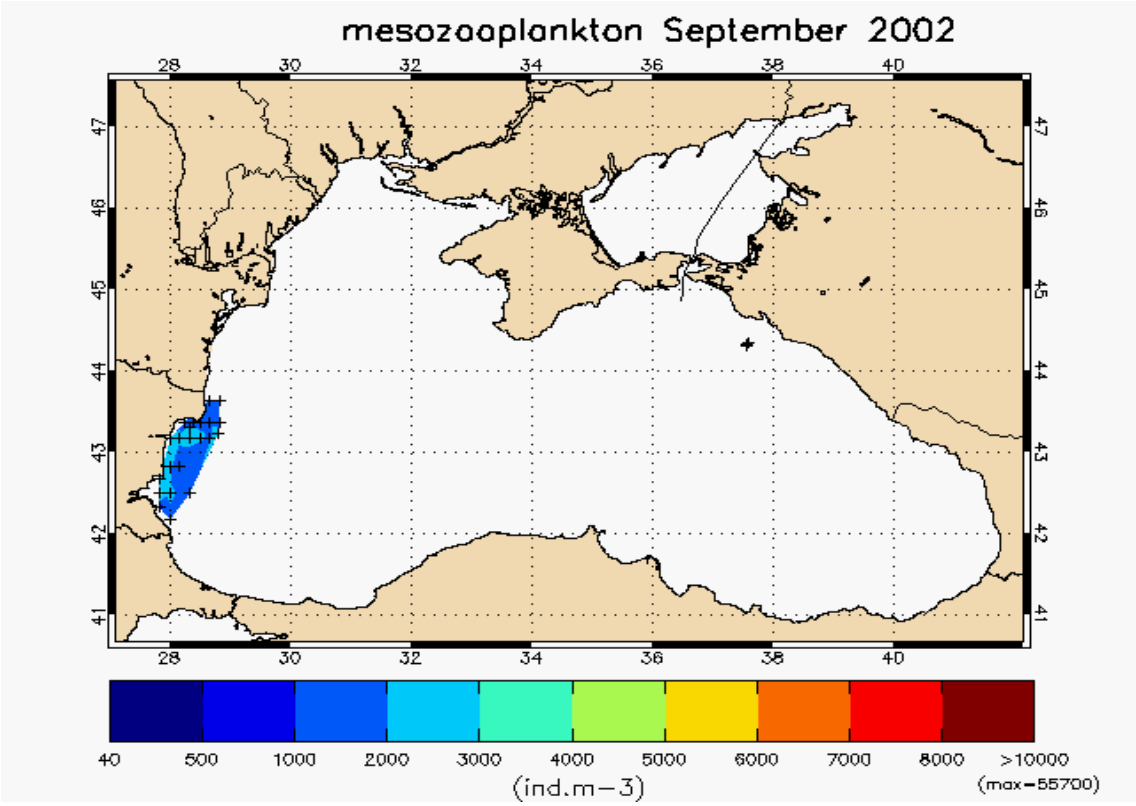


Figure 15. Total mesozooplankton numerical abundance [ind.m^{-3}] in the mixed layer above the thermocline during summer 2002 (+ sampling station)

Seen over the whole period of investigation, regularly the greater amount of mesozooplankton was registered in the North-Eastern Black Sea, while in the Western part it was of some magnitude lower. *Mnemiopsis* was maintaining a high concentration in the Western part inshore during summer 1998, which could be linked to the mesozooplankton bulks in the coastal areas (Fig. 13). When in 1999 *M. leidyi* was rare or absent, mesozooplankton was consequently much more extended along the coast in both Black Sea regions (Fig. 13). The amount of plankton fauna was reduced during the consecutive years in the Western part, while it still maintained higher values in the NEBS (Fig. 14, 15).

Large year to year fluctuations are a distinctive feature of mesozooplankton summer community, with higher values on the North-Eastern shelf in 1999 when *Mnemiopsis* was absent in the area, as well in 2001 too (Fig. 16).

During summer 1999, the average mesozooplankton numerical abundance for the WBS shelf was 10453 ± 15096 ind.m^{-3}, while at the NEBS shelf stations it reached to 14627 ± 12498 ind.m^{-3}. It seems that temperature which was relatively high in the NE part (from 22.9 to 25.4°C), provoked a pronounced increase of Cladocera species (11564 ± 11527 ind.m^{-3}) (Fig. 16). All this resulted in a great

average mesozooplankton biomass observed on the NE shelf (591.37 ± 580 mg.m^{-3}), whereas in the Western part it was much lower (124 mg.m^{-3}). Mesozooplankton quantity was higher as well offshore in the NEBS (Fig. 16).

Albeit the amount of plankton fauna in average on the shelf in the Western Black Sea was comparable to those in the NEBS during summer 2000, next year the pattern mode of oscillations was similar to 1999 (Fig. 16). Zooplankton biomass was 12 times higher in the NEBS in 2001 in comparison with WBS shelf. Like in 1999, the amount of Cladocera was 35 times more than in the NEBS shelf compared to the WBS, possibly caused by the high temperature inshore resulting in expansion of Cladocera (24.6 - 25.6°C). Contrasting was the distribution pattern of copepods, which density was three times higher in the WBS shelf in contrast to the NEBS (Fig. 16). However, the mean temperature at upper 20 meters in summer revealed a steadily increasing trend after 1998.

With respect to the year to year dynamics of mesozooplankton community in relation to *Mnemiopsis* density in the Black Sea, data for the interval 1998 - 2004 reveal more abundant mesozooplankton in the North-Eastern region compared to the Western part, quite the opposed to *M. leidyi* distribution along the regions (Fig. 17).

To summarize, species belonging to Cladocera group regularly were more plentiful in the NEBS, while the copepods dominated the WBS. Cladocera ranged from 80 to 532 ind.m^{-3} (303 ± 282 ind.m^{-3}) in the WBS during summer period of 1998-2002 (no data available 2003-2004), while it had attained to 15922 ind.m^{-3} (6066 ± 6402 ind.m^{-3}) in the NEBS. The range of Copepods was from 712 to 1466 ind.m^{-3} in the WBS (1117 ± 655 ind.m^{-3}) and from 311 to 1314 ind.m^{-3} (713± 512 ind.m^{-3}) in the NEBS.

The data analysed above give grounds to suggest the North-Eastern Black Sea as a region more favourable for mesozooplankton development during summer compared to the Western part, which most likely is related to *M. leidyi* distribution. The numerical abundance of plankton fauna in the Western Black Sea in average was about four times lower compared to the values recorded in the NEBS. However, the discussed quantitative characteristics were much lower in 1998 everywhere, whilst the ctenophore was rather well spread (Fig. 17). Quite the opposite, the mesozooplankton amount fauna substantially increased during summer of the “poor” 1999 along both Black Sea regions, concomitant with higher diversity and quantity of the major taxonomic groups.

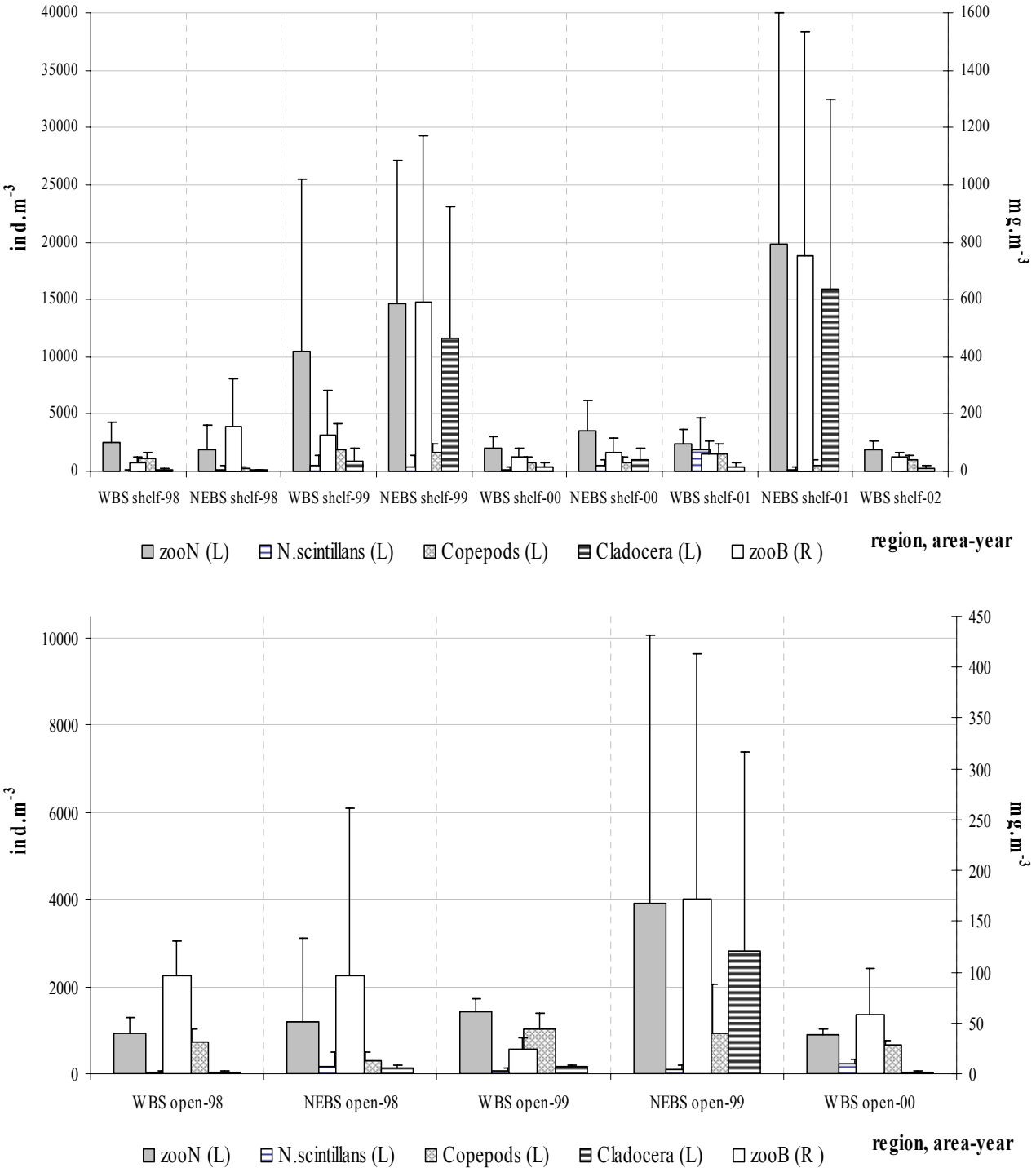


Figure 16. Interannual mesozooplankton variability in the Black Sea by regions and areas (zooN-mesozooplankton mean abundance, *Noctiluca scintillans*, Copepods, Cladocera abundance [ind.m^{-3}], zooB-mesozooplankton mean biomass [mg.m^{-3}], n=170)

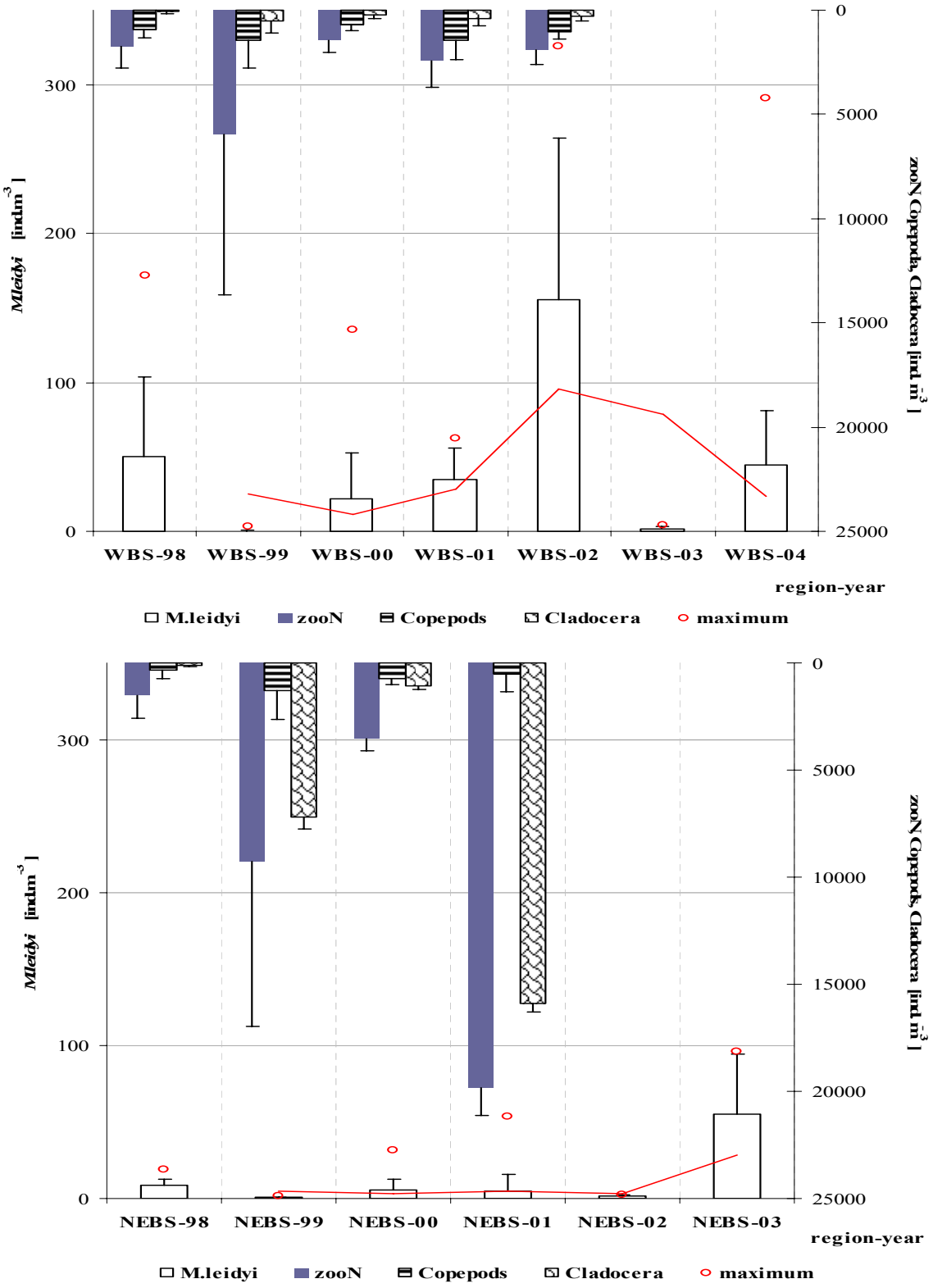


Figure 17. Interannual mesozooplankton variability in the Western (WBS) and the North- Eastern (NEBS) Black Sea; (zooN -mesozooplankton mean abundance, Copepods, Cladocera abundance [ind.m^{-3}], n=170; *M. leidyi* abundance, maximum value-symbol in red [ind.m^{-3}], n=307)

In the context of long-term historical data the period 1998 - 2004 could be considered as an exceptional due to the functioning of the prey-predator alien couple *M. leidyi-B. ovata*. Undoubtedly the period after 1998 appeared to be a transitional, under adjustment to the *Beroe-Mnemiopsis* interaction, more explicit perturbations in the Western Black Sea region (Fig. 17).

Although the mesozooplankton dynamics manifested some signs of relatively recovery all over the basin, the large inter-annual fluctuations of mesozooplankton community features could suggest instability of the recent trend in the Black Sea especially in summer (Fig. 18).

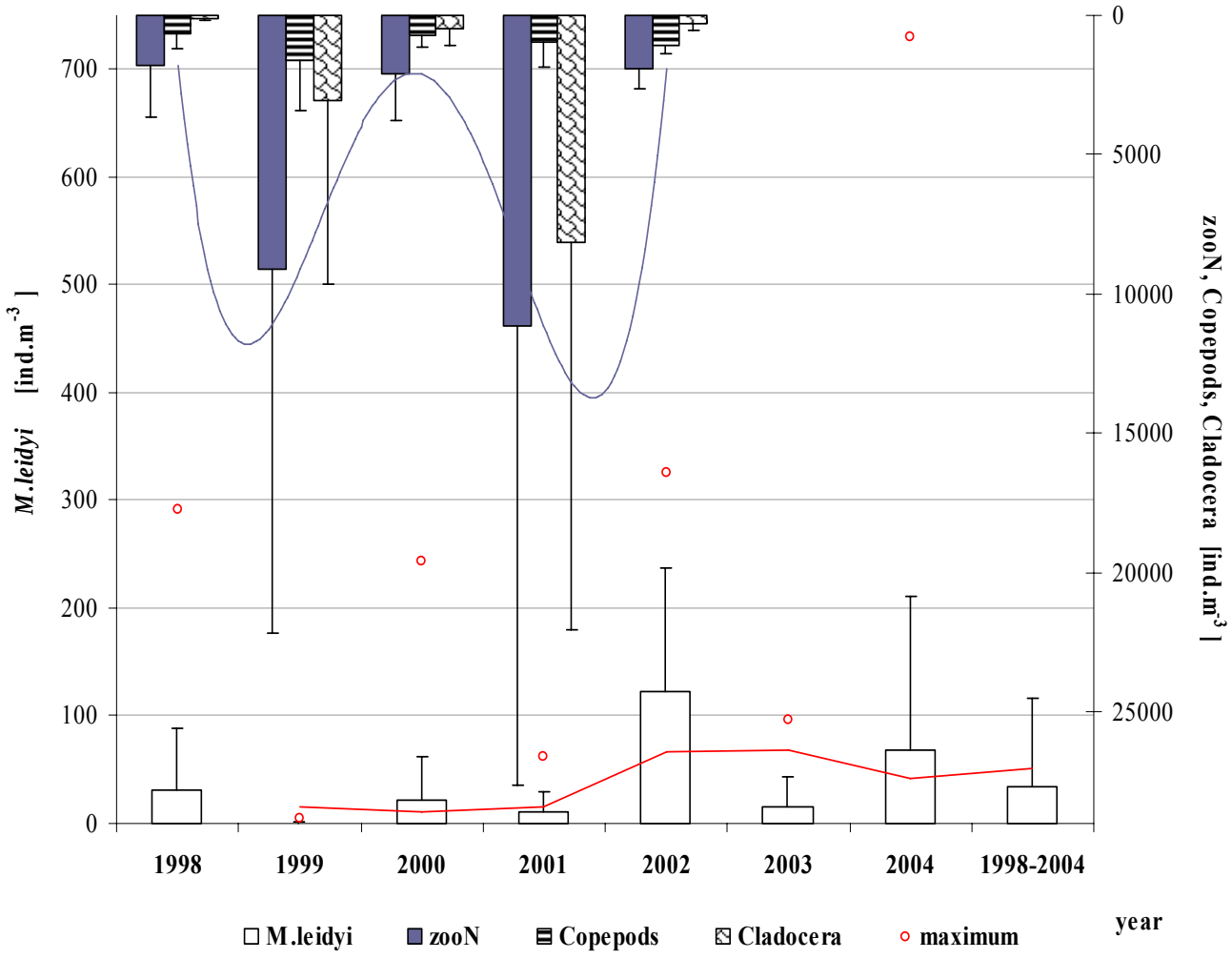


Figure 18. Interannual mesozooplankton variability during summer in the Black Sea (zooN - mesozooplankton mean abundance, Copepods, Cladocera abundance [ind.m^{-3}], n=170; *M. leidyi* abundance, maximum value-symbol in red [ind.m^{-3}], n = 334)

M. leidyi development is related to a number of environmental parameters illustrated by not so high, but significant correlation coefficients (Table 8). Significant negative correlation coefficients were found between *M. leidyi* numerical abundance and salinity (at $p < 0.05$), which presumably is linked to the hydrophysical gradient from inshore to offshore area. The growth of *M. leidyi* is favoured by higher temperature and lower salinity (Kremer, 1994). *Mnemiopsis* correlates positively with temperature, concentration of Chlorophyll *a* (from SeaWiFS) and total mesozooplankton abundance. Further, no statistically significant correlation coefficients between *M. leidyi*, Cladocera (warm-water species, generally fine filtrators) and Copepods numerical abundance was detected, which not ignore the harmful effect on the zooplankton and the functioning of the entire pelagic food web. All biological components reveal statistically significant relationships, which indeed suggest a higher vulnerability of mesozooplankton community to abiotic factors and biotic interactions in the coastal area. The negative impact of *M. leidyi* especially inshore, even at low concentrations could not be fully ignored in summer, particularly in the Western Black Sea, when *B. ovata* is absent or rare in the area.

Table 8. Correlation matrix of parameters (in red significant at $p < 0.05$, data log – transformed, see Table 2 for abbreviations)

parameter	**T**	**S**	**Chl *a***	***M. leidyi***	**Zoo N**	**COP**	**CLA**
T		-0.40	0.34	0.27	0.03	-0.01	0.24
S	-0.40		-0.74	-0.44	-0.50	-0.30	-0.24
Chl *a*	0.34	-0.74		0.45	0.47	0.20	0.40
M. leidyi	0.27	-0.44	0.45		0.27	0.23	0.17
Zoo N	0.03	-0.50	0.47	0.27		0.75	0.60
COP	-0.01	-0.30	0.20	0.23	0.75		0.23
CLA	0.24	-0.24	0.40	0.17	0.60	0.23	

The above discussed parameters were scored and narrowed down by PCA, which was applied to identify the most relevant combination of factors. The matrix was based on a data array of the following parameters: Temperature (T), Salinity (S), mesozooplankton abundance (Zoo N), Chlorophyll *a* concentration (Chl *a*), and numerical abundance of *M. leidyi*, Copepods (COP) and Cladocera (CLA) ($n = 334$). We present the first three extracted components (PC 1), (PC 2) and (PC 3), to which most ecological significance could be attached. They explained 74.8 % of the total variance.

After normalizing the factor loadings, a rotation at maximizing the variance (varimax rotation) was used. The first component PC 1 (a loading of 30 % in the total variance) corresponds to increase in mesozooplankton abundance, Cladocera and copepods numerical abundance (*mesozooplankton* component). PC 2 (25 %) correlates positively with increase of *M. leidyi* and Chlorophyll *a* (e.g. *grazing* component). PC 3 (19 %) corresponds to a decreasing in temperature and increase of salinity (*abiotic* component) (Fig. 19).

The discrepancy between the regions was mainly in respect to *Mnemiopsis* occurrence and Chlorophyll *a* (Table 9). The PCA plot of the determinant scores shows a clear discrimination between the three regions along the axis PC 2 (grazing) (Fig. 20). North-Western and Western Black Sea correspond to increase of Chlorophyll *a* and *M. leidyi*, just the opposite to the North-Eastern region.

Table 9. SeaWiFS-derived mean Chlorophyll *a* concentration ($mg.m^{-3}$) by regions (NEBS-North-Eastern; WBS-Western; NWBS-North-Western Black Sea), areas (shelf < 200 m, open sea > 200 m depth) and years (descriptive statistics, n-number of valid cases)

Region, area-year (n)	**Chl *a* [$mg.m^{-3}$] mean value ± stdev**
NEBS	
shelf-98 (10)	0.789 ± 0.261
open-98 (24)	0.603 ± 0.141
shelf-99 (10)	0.806 ± 0.386
open-99 (32)	0.713 ± 0.218
shelf-00 (16)	0.558 ± 0.126
shelf-01 (40)	1.017 ± 0.860
shelf-02 (4)	0.670 ± 0.008
open-02 (2)	0.658 ± 0.019
Average (138)	0.773 ± 0.520
WBS	
shelf-98 (17)	1.788 ± 0.662
open-98 (5)	1.038 ± 0.199
shelf-99 (18)	2.708 ± 1.021
open-99 (5)	0.916 ± 0.425
shelf-00 (26)	1.803 ± 0.462
open-00 (7)	0.924 ± 0.196
shelf-01 (8)	2.120 ± 0.762
shelf-02 (14)	1.773 ± 0.629
shelf-03 (10)	0.731 ± 0.260
open-03 (2)	0.473 ± 0.227
shelf-04 (23)	1.722 ± 0.674
open-04 (3)	1.0199 ± 0.502
Average (138)	1.703 ± 0.833
NWBS	
shelf-04 (27)	2.782 ± 1.924
All total (303)	1.376 ± 1.071

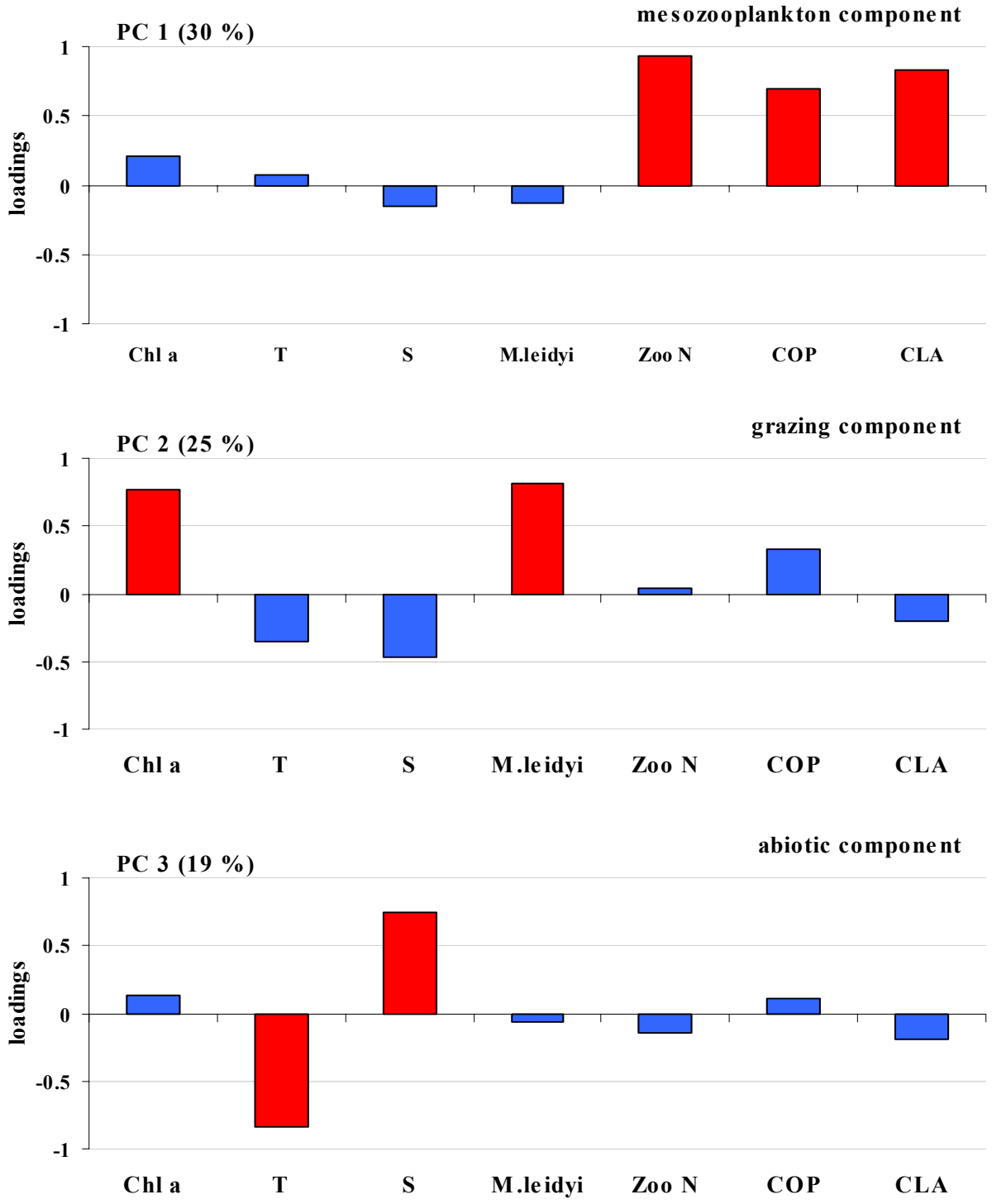


Figure 19. Principal Component Analysis: Plot of PC loadings of the first three components (PC 1, PC 2, PC 3) (varimax normalized, loadings marked in red significant at p >0.7)

The large variability of hydrophysical (temperature, salinity) and biological parameters at the sampling stations on the shelf certainly lead to more complex interactions and gradients inshore. That is why due to the great dispersion of determinants it is difficult to discriminate the regions along the other two axes- PC 1 (mesozooplankton component) and PC 3 (abiotic component) (Fig. 20).

PC's scores were plotted to illustrate more clearly the distribution of determinants in between the regions, areas and years (Fig. 20, 21, 22). Considering that PC 2 is the main descriptor, the results shows high significance of grazing component (PC 2) in the Western and North-Western regions contrasting to the NEBS (Fig. 21).

The analysis suggests a negligible role of the grazing component (PC 2) for the shift in zooplankton community (PC 1) in the North-Eastern Black Sea. Almost 95 % of plotted scores refer to low *M. leidyi* and Chlorophyll *a* in the NEBS, while in the WBS only 40 % of the scores covering mainly offshore and some of the shelf stations particularly in 1999 and 2003 (Fig. 21). Nonetheless, according to SeaWiFS derived mean concentration of Chlorophyll *a* (PC 2) in 1999 was higher than the previous year in both investigated regions (Table 9).

Regarding mesozooplankton component (PC 1), a great time-spatial heterogeneity was typical of mesozooplankton distributions (Fig. 21, 22). Plotted scores with low zooplankton refer to 1998, 2000 and to offshore stations in both regions, together with 2002 in the WBS when *Mnemiopsis* occurred significantly (Fig. 21).

In respect to abiotic component extracted by the analysis (PC 3), which correlates to decreasing of temperature and high salinity the distribution of the plotted scores demonstrates discrepancy along the gradient shelf – open sea area. For both Black Sea regions, scores plotted for summer 1998, 1999 are projected at coordinates corresponding to the lower temperature, higher salinity (Fig. 21).

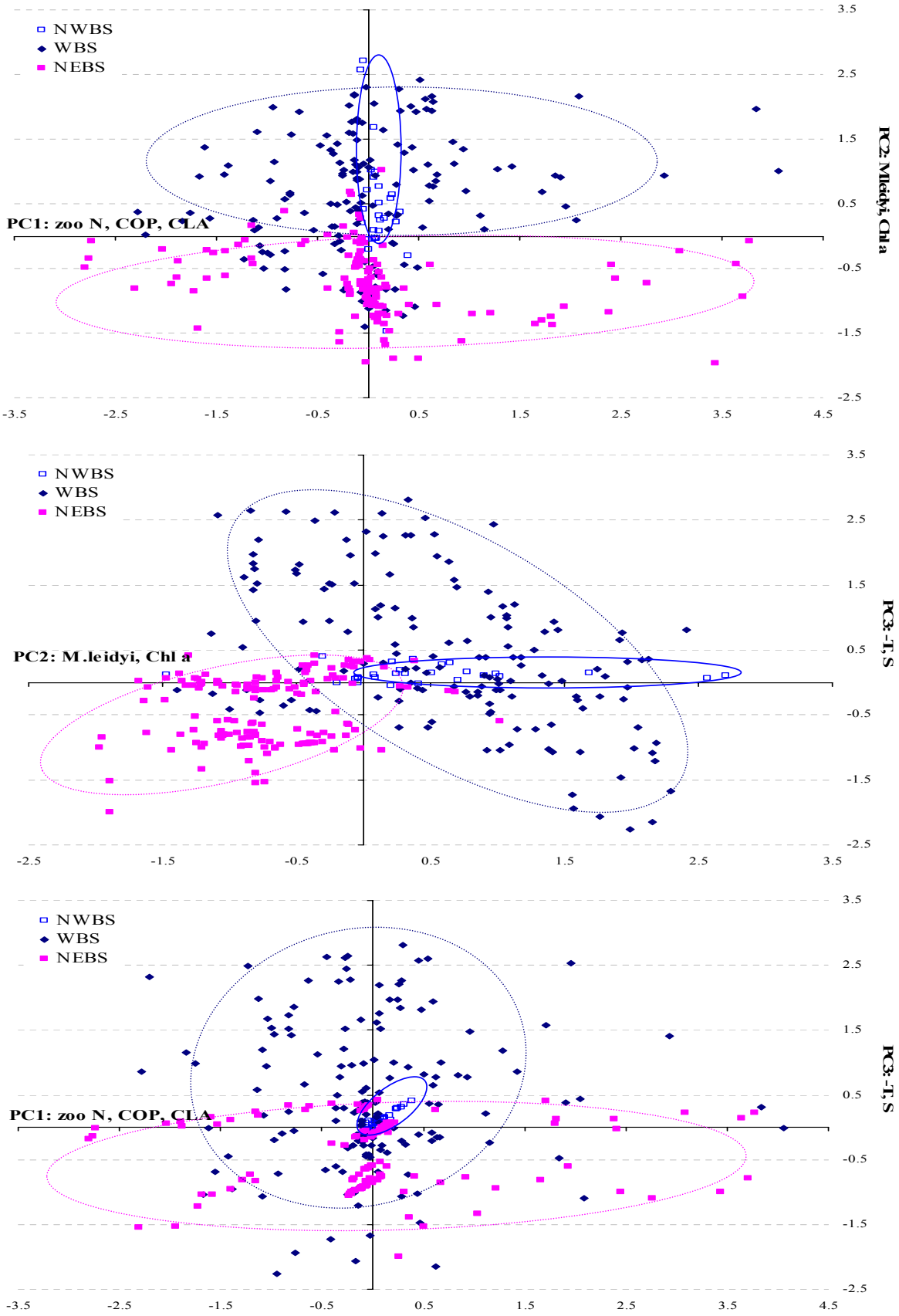


Figure 20. Scatter plot of PC scores by regions

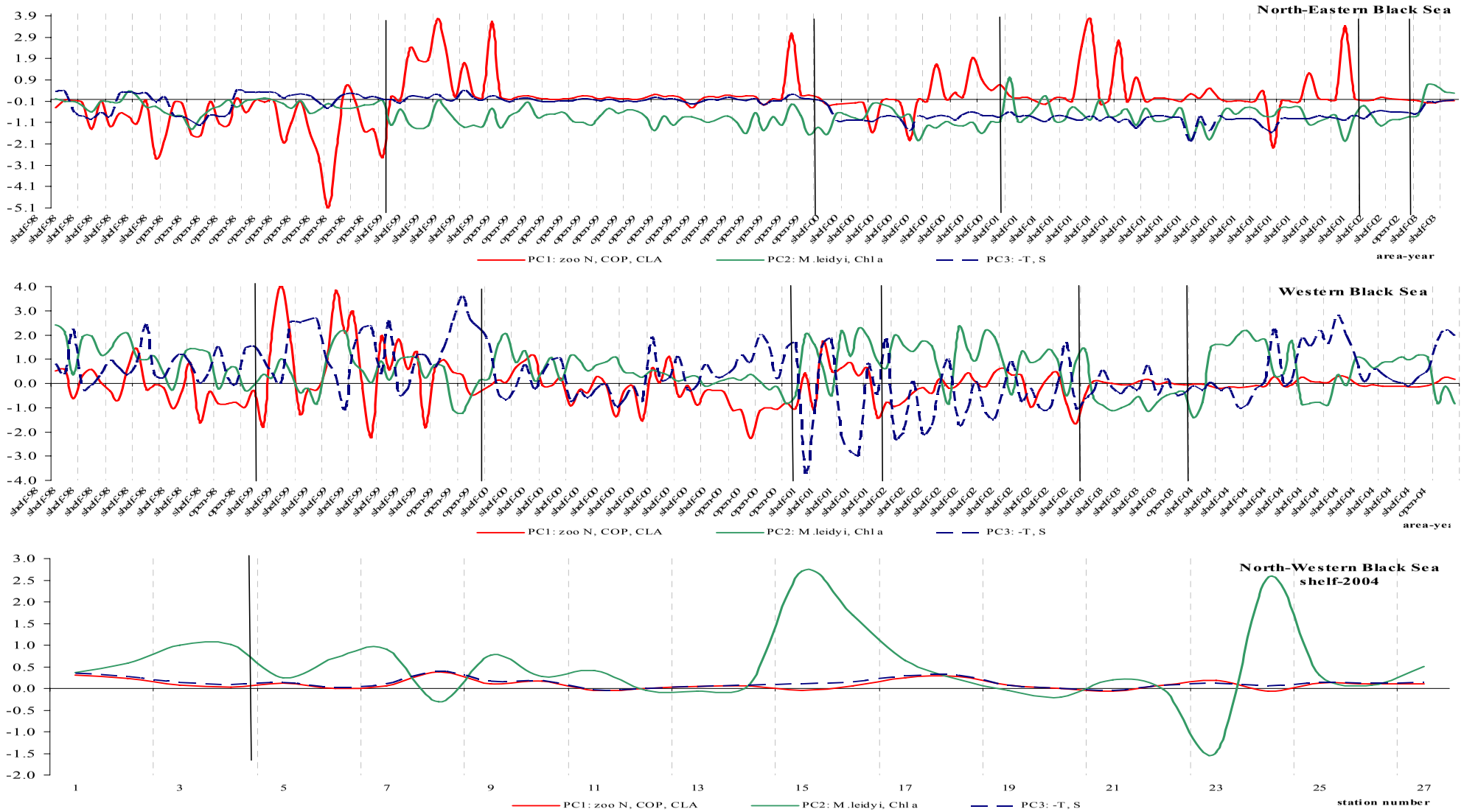


Figure 21. Plot of PCA loadings by regions, areas and years

PCA projection of yearly means of 1998, 2000 and 2002, correspond to lowest zooplankton, contrasting with 1999 and 2001 (high zooplankton component-PC 1) (Fig. 22). In respect to abiotic component (PC 3), yearly means projections match with highest temperature are those for 2000 to 2003, dissimilar to 1998, 1999 and 2004. Discrepancy between the years was above all to the *grazing* component PC 2 (*Mnemiopsis* and Chlorophyll *a*). The yearly means of 1999, 2001 and 2003 are projected at coordinates corresponding to the lowest grazing, which coincide with classifying those years as "poor". The exception is 2000 which projection follows to the same group certainly as a result of high Chlorophyll *a* contribution to the PC 2.

Discrepancy between the years 1998-2004 was primarily in respect to occurrence of *Mnemiopsis*, temperature and numerical abundance of Cladocera at shelf stations. By reducing grazing pressure on phytoplankton, *M. leidyi* implicitly provoked enhanced primary production. Mesozooplankton community inshore is more vulnerable to *M. leidyi* impact in summer due to a time-lag in *Beroe* occurrence and reproduction in the coastal area (Finenko et *al*., 2003; Kamburska et *al*., 2003). The PCA results give evidences that grazing (PC 2) and its effect could explain the shift in mesozooplankton during the last years (Fig. 21, 22). This stated particularly for the processes in the NWBS and WBS regions, whereas in the NEBS the abiotic component is a key factor for the plankton dynamic (Fig. 21).

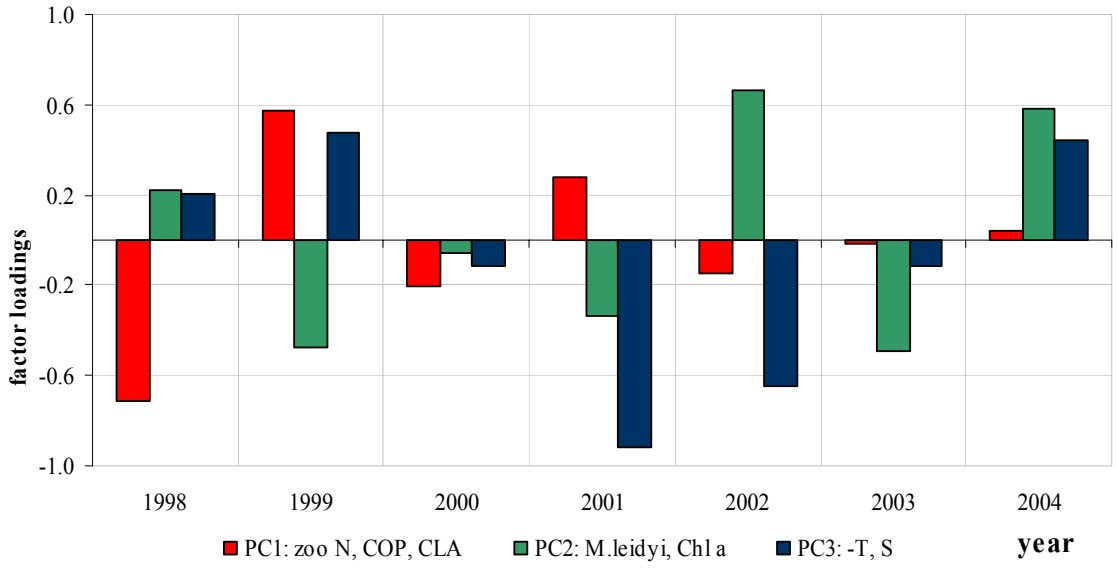


Figure 22. Plot of PC's loadings by years

3.3. Long-term trends

Long-term studies offer a viewpoint on the roles of species or functional groups in ecosystems, especially on the response of ecosystems to environmental change. To reveal how the recent period fits in terms of long term mesozooplankton dynamics, a sampling site in the coastal zone of the Western Black Sea was selected (a monitoring station at 3 miles off the Bulgarian coast, off cape Galata). Long-term dynamics of numerical abundance of dominant Copepods and Cladocera [ind.m^{-3}], *M. leidyi* [ind.m^{-3}], *B. ovata* [ind.m^{-3}], temperature and salinity revealed large interannual fluctuations in the period 1967-2004 (Fig. 23, 24).

The large-scale trends in temperature and salinity during summer are apparent from the anomalies (deviations from the long-term average for the whole 38 year period). After a relatively warm cycle during the 1960s-1970s, a tremendous decrease of temperature related to the climate variability in the Northern hemisphere (Oguz, 2005) led to the coldest period- the 1980s (Fig. 23). The negative temperature anomaly was more than 1.5 times the standard deviation. Following the 1990s-2000s, the anomalies reveal a warming trend of 2.5-3 degrees than the average. On the contrary, the late 1990s-2000s are with negative salinity anomaly (Fig. 23).

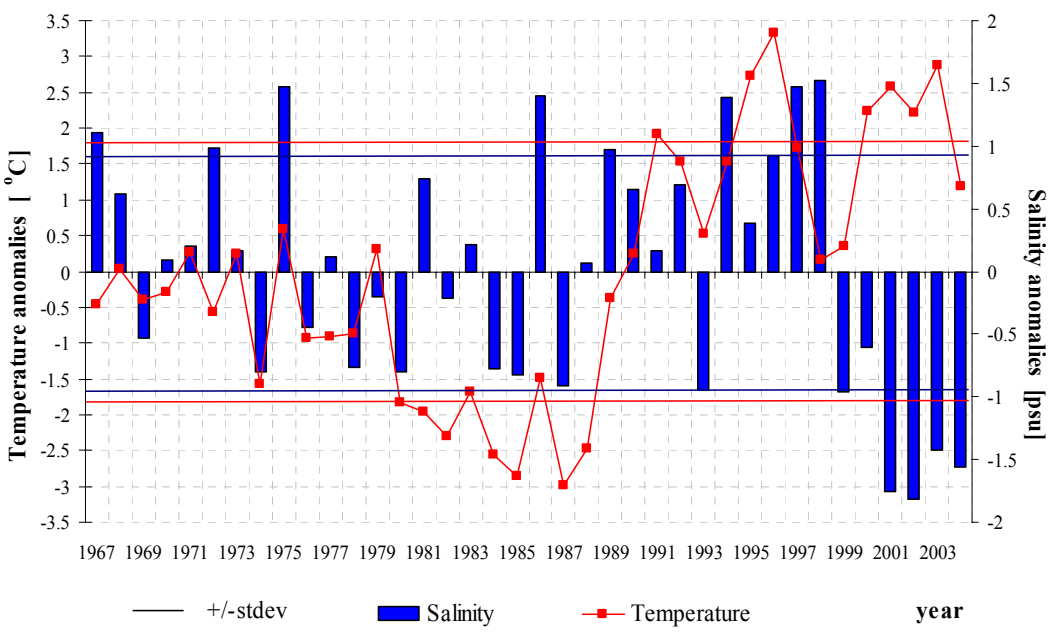


Figure 23. Long-term variations of summer temperature and salinity anomalies in the upper 10 meters layer at 3 miles station off cape Galata (Western Black Sea) for the period 1967-2004

In the period 1995-2000 gradually the winters were becoming warmer, the springs colder and the summers were short and hot. The long-term averages show spatially a minimum of salinity in front of the Cape Galata to 10 miles offshore (Dineva, 2005).

The 1980s-1990s were characterized by remarkable variations of the discussed biotic parameters too (Fig. 24). In contrast to the period 1967-1980, the average abundance of both taxonomic groups sustained at a lower level during the 1980s. This level was again reduced during the 1990s due to the occurrence of *M. leidyi*, before its predator *Beroe* appeared (Fig. 24). The 1980s-1990s were characterized by irregular inter-annual fluctuations of mesozooplankton abundance, which appeared related to the changes of abiotic parameters, but particularly were more evident after the introduction of *Mnemiopsis* (Fig. 23, 24). Altered mesozooplankton dynamics during the late 1980s-1990s can be seen as an adequate response to the modified environmental conditions caused by the drastic change in the climate regime of the 1990s and *Mnemiopsis* pressure too.

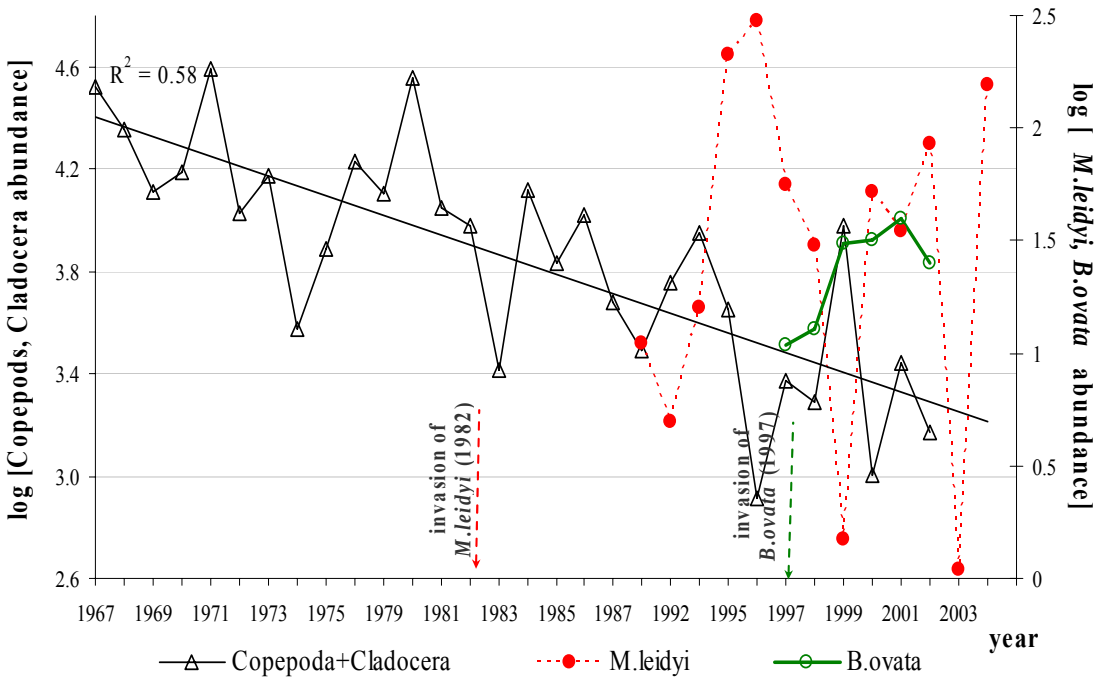


Figure 24. Long-term variability of selected biotic parameters (log transformed) at 3 miles station off cape Galata (Western Black Sea) during summer period 1967-2004

In the context of long-term historical data the investigated period 1998-2004 could be considered as exceptional due to the functioning of the prey-predator alien couple *M. leidyi*-*B. ovata*. Therefore during the summer season of 1998-2004, the abundance of *M. leidyi* sustained at a level much lower than the concentrations typical for the late 1980s (Shiganova et *al*., 2001*b*). Faced with predation, *Mnemiopsis* was reduced during the last years, but even if *M. leidyi* was rare in 1999 and 2003 in the area, it was found again in relatively high concentration in 2002 and again in 2004 in the Western Black Sea (Fig. 24). The post-invasion impact of *B. ovata* on *M. leidyi*, native medusa *A. aurita* and

mesozooplankton dynamics remains still a question under consideration. Signs of a relative recovery of Black Sea zooplankton dynamics and diversity have been reported, which could be interpreted as a result of the *Beroe* predation on *Mnemiopsis* (Finenko et *al*., 2000; Shiganova et *al*., 2001*d*; Kideys, 2002; Kideys et *al*., 2005), but not ignoring the role of large-scale weather patterns on the pelagic Black Sea ecosystem too (Niermann et *al*., 1999; Moncheva et *al*., 2001; Oguz, 2003). More, the pronounced increase of Cladocera species certainly is caused by the augmented temperature and sharp drop of salinity (Fig. 23).

Even if signs of somewhat recovery were manifested by the plankton fauna all over the basin after the invasion of *Beroe* (Shiganova et *al*., 2000; Finenko et *al*., 2003; Kamburska, 2004), the large year to year fluctuations might suggest instability of the recent trend especially in summer. The period after 1998 appeared to be a transitional, in terms of the adjustment to the *Beroe- Mnemiopsis* interaction. The results given above provide further arguments that the negative impact of *M. leidyi* in the Black Sea, even at low concentrations could not be fully ignored most of all in summer, when *B. ovata* is absent or rare in the area.

Erratic environments (unstable and/or unpredictable environments) are characterized by species with a r-strategy, e.g. species with rapid development, high intrinsic rate of increase, early maturity and reproduction, high resource thresholds, short lifespan, high productivity. Definitely, the invader *Mnemiopsis leidyi* is a typical r-strategic species. The broad range of biological and ecological characteristics of *M. leidyi* assures a great capability to adapt to quickly changing environment. The settlement of *B. ovata* is reducing *Mnemiopsis* population vigour, but still it has exerted the pelagic food web in summer (Shiganova et *al*., 2001*b*; Kamburska, 2004). Furthermore, the food web in this case is particularly favouring the so-called “dead end” species of gelatinous organism.

A distributional shift of *M. leidyi* along the three investigated regions was apparent. The spreading of the species appeared to be related to environmental parameters confirmed by significant correlation coefficients. So far as *Mnemiopsis* is unable to reproduce in oligotrophic environments (Harbison, 2001), *M. leidyi* occurrence and frequency in the Black Sea certainly depend on trophic status. The greatest amount of the ctenophore constantly recorded in the uppermost eutrophicated North-Western and Western Black Sea in contrast to the North-Eastern part confirmed this species distinctiveness. Undoubtedly the presence/absence of *M. leidyi* (also its concentration) is a reliable bioindicator not only reflecting on biodiversity, but also on the environmental quality. The occurrence of the invasive species potentially causes changes and imbalance to diversity and stability of the ecosystem, which could be irreversible for the area.

Therefore *Mnemiopsis* is a key species which trends in abundance and distribution should be constantly monitored in the vulnerable Black Sea ecosystem.

4. CONCLUSIONS

The results for the time-space distributional pattern of the invasive ctenophore *Mnemiopsis leidyi* in the Black Sea in relation to some environmental factors give grounds to synthesize the following conclusions, recommendations and gaps in knowledge:

- ✓ During summer season of the period 1998-2004, *M. leidyi* reveal great spatial-temporal variability in the Black Sea, reached to maximum of 729 ind.m^{-3}. A gradient in *M. leidyi* distribution mode along the three investigated regions was apparent- the greatest amount of species was permanently registered in the uppermost eutrophicated North-Western and Western Black Sea, whereas it was rare in the North-Eastern part;
- ✓ *Mnemiopsis* constantly prevailed at the shelf stations (<200 m depth) contrasting to open sea waters (> 200 m depth). Thus some coastal areas could be considered as "hot spots" caused by regularly retained significant amounts of *Mnemiopsis* (bloom concentration). Such areas at risk in the Western Black Sea are the coastal stations at transects Kaliakra, Galata and Burgas. The highest value of *Mnemiopsis* for the whole investigated period was recorded at a sampling station close to Danube delta (the North-Western Black Sea);
- ✓ Considering *M. leidyi* density, the years of the interval 1998-2004 could be classified as: "normal" years -1998, 2000, 2002 and 2004, since *M. leidyi* abundance sustained at a level much lower than blooming concentrations typical for the late 1980s. As "poor" years are identified 1999, 2001 and 2003- the ctenophore was rare, almost absent, maintaining mean abundance less than 10 ind.m^{-3} (a threshold value for medusa bloom). *Mnemiopsis* was lower even during the "normal" years in the North-Eastern region compared to North-Western and Western Black Sea, at a level of not more than 10 ind.m^{-3} in average. It seems *Mnemiopsis* presenting a cycle of high /low abundance or presence/absence, or succession of poor–normal -rich years, the duration of which periods is irregular and not easy to be predicted;
- ✓ Ecological assessments of plankton fauna community structure, together with applied statistical analyses suggest strongest impact of the invasive species in the North-Western and Western Black Sea, especially on the shelf. In respect to inter-annual fluctuations of mesozooplankton community, the obtained results reveal regularly higher mesozooplankton quantity in the North-Eastern compared to the Western Black Sea, such the opposed to *M. leidyi* distribution in the regions. The observed trend of roughly 5 times lower mesozooplankton abundance in the WBS shelf for the period 1998-2004, seems to be related to the widespread *M. leidyi* in the area. The analyses suggest as more favourable for summer mesozooplankton development the

North-Eastern Black Sea, compared to the Western part, supported by the Principal Component Analysis;

- ✓ The first three components extracted by the PCA to which most ecological significance could be attached (73 % of the total variance) could be described as *mesozooplankton component* (PC 1 corresponds to increase in mesozooplankton and Cladocera numerical abundance); *grazing component* (PC 2 correlates positively with increase of *M. leidyi* and Chlorophyll *a*); and *abiotic component* (PC 3 corresponds to a decrease in temperature and increase of salinity);
- ✓ The discrepancy between the regions was mainly in respect to *Mnemiopsis* occurrence and Chlorophyll *a* concentrations. PCA results illustrate a significance of grazing pressure (PC 2) for the shift in mesozooplankton dynamics (PC 2) in the Western and North-Western Black Sea (high Chlorophyll *a* and *M. leidyi*), whereas in the North-Eastern part, abiotic component (PC 3) is a key controlling factor for the plankton fauna;
- ✓ The discrepancy between the years was mostly due to the *grazing* component (*Mnemiopsis* and Chlorophyll *a*), temperature and Cladocera at shelf stations. PCA projection of yearly means of "normal" 1998, 2000 and 2002, corresponds to lowest zooplankton. Yearly means of 1999, 2001 and 2003 are projected at coordinates corresponding to lowest grazing and high zooplankton, which coincide with classifying those years as "poor". In respect to abiotic component, yearly means projections with highest temperature are 2000 to 2003, unlike to 1998, 1999 and 2004;
- ✓ The great variability of hydrophysical (temperature, salinity) and biological parameters on the shelf certainly lead to more complex interactions and gradients inshore. Biological components demonstrate statistically significant relationships, which suggest a higher vulnerability of mesozooplankton community to abiotic factors and biotic interactions inshore confirmed also by the long-term trends in the coastal zone;
- ✓ Despite of large inter-annual variability, *Mnemiopsis* still remains a key factor controlling mesozooplankton dynamics particularly in summer. A prey-predator relationship of the alien couple *M. leidyi -B. ovata* gives an opportunity to plankton fauna to recover (e.g. increased abundance, biomass and diversity). The period after 1998 appeared to be a transitional under adjustment to *Beroe- Mnemiopsis* interaction, with more explicit perturbations in the Western Black Sea. In the context of the long-term dynamics, quite high *M. leidyi* densities in 2002 and 2004 in the North-Western/Western parts, together with the abiding oscillations of *B. ovata* and the dominant mesozooplankton groups, is alarming that the hazardous impact of

Mnemiopsis even at low concentrations could not be fully ignored most of all in summer, when *B. ovata* is absent or rare in the Black Sea;

- ✓ Long-term trends provide insights that other factors besides trophic interaction control the Black Sea plankton fauna in the coastal zone (e.g. climate forcing, anthropogenic pressures). The 1980s-1990s were characterized by irregular inter-annual fluctuations of mesozooplankton abundance, which appeared related to the changes of abiotic parameters, but more evident after the invasion of *Mnemiopsis*. The alterations in mesozooplankton community during the late 1980s-1990s could be seen as an adequate response to the modified environmental conditions caused by the drastic changes in the climate regime and *Mnemiopsis* pressure;
- ✓ Further investigations, coupling biological and physical interactions are needed, as the mechanisms triggering *Mnemiopsis* "poor", "normal" or "rich" years are still unclear, and questioned the role of *Beroe* as the only underlying mechanism of zooplankton recovery. Time-space variability of pelagic communities should be analyzed also with respect to abiotic factors (temperature, light, nutrient concentrations and hydrodynamics)

M. leidyi occurrence (presence/absence, concentration) is a reliable *indicator* not only reflecting on biodiversity, but also the ecological quality of the environment. *Mnemiopsis* spreading is related to various environmental parameters. The broad range of its physiological and ecological characteristics of the species assures a great capability to adapt quickly to shifting environment. The occurrence and frequency of the species in the Black Sea undoubtedly depend on trophic status too, confirmed also by strong positive correlation with Chlorophyll *a* concentration (SeaWiFS). The greatest amount of the ctenophore constantly recorded in the uppermost eutrophicated North-Western and Western Black Sea in contrast to the North-Eastern part (no nutrients enrichment) make evident also that intrinsic characteristic to the species.

Mnemiopsis faced all criteria to be included in the List of Worst invasive alien species threatening European biodiversity and marine ecological quality. It has caused a damaging impact on diversity and ecosystem stability through altering the Black Sea ecosystem structure and functioning, replacing indigenous species and provoking further introduction of aliens (*Beroe ovata* introduction in the late 1990s). Besides, *M. leidyi* has negative effect on human activities and socio-economic interests, which make crucial the monitoring of ctenophore outbursts and assessment of the relationship with other destabilizing factors in the Black Sea Region.

LIST OF FIGURES AND TABLES

FIGURES

Figure 24. Long-term variability of selected biotic parameters (log transformed) at 3 miles station off cape Galata (Western Black Sea) during summer period 1967-2004

TABLES

ACKNOWLEDGEMENTS

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Abstract

The report aims to address the ecological issue of the invasive species. The human-mediated invasions, often referred to 'biological pollution' are a worldwide problem that is increasing in frequency and magnitude, causing significant damage to the environment, economy and human health. Bioinvasions have strong impact on biodiversity and ecosystem functioning and stability. They are ranked as the second most important threat to biodiversity (after habitat destructions) by the World Conservation Union. "Trends in invasive alien species" is recognized as indicator of marine biodiversity and ecosystem health assessment, proposed and included in the EU set of headline biodiversity indicators (SEBI-Streamlining European 2010 Biodiversity Indicators) and EEA core set of indicators.

'Numbers and cost of alien invasions' is one of the indicators for assessing progress towards the 2010 target (UNEP/CBD/SBSTTA/10/INF/17, 2005). More, 'Inventory of the occurrence, abundance and distribution of non-indigenous species presented in the region/sub-region' is proposed as biological element in the initiative of the EC, the Marine Strategy Directive (COM, 2005). Some policy gaps remain in the area of prevention and control of invasive alien species. For this purpose, a key objective is to develop specific actions, including an early warning system.

A case study presented is an assessment of distributional mode, long-term dynamics and trends of the invasive ctenophore Mnemiopsis leidyi (Agassiz, 1865) in the Black Sea. This species has led to tremendous ecosystem changes and substantial economic losses in the late 1980s-1990s and it has been recognized as a problem of main ecological concern for the sustainable development of the region, together with the high level of anthropogenic forcing on the Black Sea ecosystem. Data from three Black Sea regions are combined, summarized and recent information on M. leidyi population distribution and occurrence, mesozooplankton pattern and the differences in between the regions is provided.

This report gives practical information to struggle with analogous invasions in other European Seas, using the example of the Black Sea. It could contribute to the debate on the development of EU headline biodiversity operational indicators in achieving the EU target of halting the loss of biodiversity by 2010.

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