

Research Article

The non-native copepod *Oithona davisae* (Ferrari F.D. and Orsi, 1984) in the Western Black Sea: seasonal and annual abundance variability

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Abstract

A new cyclopoid copepod species, *Oithona davisae* was discovered during regular monitoring along the western coast of the Black Sea in 2009–2012. In the short period since its discovery off the Bulgarian Coast, *O. davisae* populations have increased to become one of the dominant zooplankters, contributing up to 63.5–70.5 % of total mesozooplankton numbers in the Varna Bay and adjacent open sea waters. This species thrived in early autumn with a maximum density of 43818 ind.m³ in the eutrophic Varna Bay, but seasonal and annual abundance fluctuated widely during the investigation period. Temperature variability, changes in the phytoplankton community composition, and decreased abundance of gelatinous plankton were investigated as possible drivers for rapid increase in the new established population *O. davisae* in the Black Sea.

Key words: alien species; abundance fluctuations; zooplankton; Varna Bay

Introduction

Small copepods, such as those of the cyclopoid family *Oithonidae*, are among the most ubiquitous and abundant metazoans in the oceans of the world (Gallienne and Robin 2001; Turner, 2004). Oithonids contribute significantly to secondary production and are an important component of marine trophic chains, presenting a food source for planktivorous fish and many predatory fish larvae (Calbert and Agusti 1999; Saiz et al. 2003; Turner 2004).

Two representatives of *Oithonidae*, namely *Oithona similis* (Claus, 1866) and *Oithona nana* (Giesbrecht, 1893), are thought to be native to the Black Sea. *O. similis* is a deepwater inhabitant that can perform large vertical migrations and is common in the plankton community (Vinogradov 1989). *O. nana*, is an eurythermic

copepod that was widely distributed in the region in the 1970's and 1980's, where it was present at high densities in the surface layer. Since the beginning of the 1990's, however, O. nana has totally disappeared from the zooplankton community, apparently due to predation by the invasive ctenophore Mnemiopsis leidvi (Agassiz, 1865), which became established at this time (Pereladov 1988; Shushkina et al. 1990). Since then, the zooplankton community has been characterized as ctenophore-dominated with devastating consequences on the ecosystem, most notably a major decline of mesozooplankton numbers and fish stocks (Shiganova 1997; Zaitsev and Mamaev 1997). In 1997, the carnivorous ctenophore Beroe ovata (Mayer, 1912) was introduced into the Black Sea. It feeds on other ctenophores and has caused a reduction in the concentration of M. leidyi (Konsulov and Kamburska 1998; Kideys and Romanova 2001).

Since 2001. a new species of Oithonidae initially described as Oithona brevicornis, has been collected in Sevastopol Bay, Crimea, Black Sea (Zagorodnyaya 2002; Gubanova and Altukhov 2007). Temnykh and Nishida (2012) recently reassessed the species' identification and concluded that the species' was actually Oithona davisae (Ferrari and Orsi, 1984). O. davisae inhabits eutrophic embayments (Uve and Sano 1995; Almeda et al. 2010) and is indigenous to Japan and the China Seas, and other coastal areas (Razouls et al. 2012). It is an invasive species along the west coast of the US (Ferrari and Orsi 1984) and the Spanish Mediterranean (Saiz et al. 2003). Most likely the vector of introduction to the Black Sea is from the ballast waters of ships (Selifonova 2009).

The aim of this study was to examine the seasonal and inter-annual variation in abundance of *O. davisae* in the western part of the Black Sea. Variation in abundance and possible controlling environmental factors were examined in both native and introduced parts of its range. Recent plankton community changes in the Black Sea were assessed to gain insight about possible driving factors for the success of this newly established invasive species.

Material and methods

Zooplankton samples were collected at 31 stations in the Western Black Sea, between March 2009 and March 2012, including Varna and Bourgas Bays and open sea waters (Figure 1). Information about the collected samples, including sampling localities, number of stations and time intervals is presented at Table 1. In 2009 the sampling took part in March, June, September and November, while in 2010 the monitoring program encompassed March, April, July, August, September and December. During 2011 the sampling occurred in April, May, July, August, September and October. A minimum of four common stations in each sampling area were visited during the monitoring, while duplicate tows were performed at each 2nd or 3rd station, depending on the total station number.

Mesozooplankton was collected by vertical hauls using a "Juday" plankton net, (provided with a flowmeter), with a 36 cm diameter opening and mesh size of 150 μ m. Sampling was carried out from the whole water column. Samples were preserved in 4% formaldehyde and processed by the methodology for zooplankton studies in the Black Sea of Korshenko and Aleksandrov (2006, draft, pers.com.) and HELCOM Annex C 7: Mesozooplankton. According to the methodology the sample was homogenized, and a calibrated Stempel-pipette with a 1-ml sampling chamber was used for the first sub-sampling, and quantitative and qualitative processing was performed in a Bogorov's chamber. A minimum one additional sub-sample was treated, with a volume of 5-10 ml to obtain information on the species composition and abundance. In the subsample(s) all plankters were counted until each of the three dominant taxonomic groups reached 100 individuals. For estimation of large animals' numbers, the whole sample was observed under the microscope. All species were identified taxonomically to the species level except of the meroplankton larvae and rotifers. The species abundance was expressed as a number per cubic meter.

Mainly adult and copepodid stages of *Oithona* were found in the samples as the net mesh size was not appropriate for quantitative collection of nauplia stages.

Results and discussion

O. davisae specimens were first found along the Bulgarian coast in September 2009 (Table 1). Specimens were collected in several stations including the Bay of Varna and in the central west coastal waters. Abundance ranged between 128-1985 ind.m⁻³ with a mean value of 931 ind.m⁻³ for the whole investigated area. Average abundance of O. davisae during November 2009 was 1.8 times that of September in both localities - Varna Bay and open sea. During the next year, the species was detected from July to December with surface water temperatures ranging from 24.5 to 12.8°C, respectively. In 2011, O. davisae was present when sampling commenced in April at surface water temperatures of 14.9 to 16.4°C. Unlike 2009 and 2010, specimens of O. davisae were detected during March 2012 in the Bay of Bourgas, at a water temperature of 7.3°C. Sample collection was not, however, sufficient to assess the full tolerance of this species to low water temperatures, which might lead to almost all-year-round presence in the embayments.

O. davisae comprised up to $17.7\% \pm 5.1$ (SE) of the total mesozooplankton abundance for the studied period, with highest percentages of



Figure 1. Investigated areas along the western coast of the Black Sea (A) and (B) close-up. The Figure was prepared using Ocean Viewer (Schlitzer 2011).

Table 1. Sampling frequency, range of abundance (minimal – maximal values; ind.m⁻³) of *Oithona davisae* (OD) and total mesozooplankton (MZP), and percentage OD of total MZP abundance.

| Date | Locality | Number of stations | OD Range | OD Average density | MZP Range | MZP Average density | OD (%) of Total MZP |
|---------|-------------|--------------------|------------|--------------------------|--------------|------------------------|------------------------|
| 03.2009 | Varna Bay | 8 | - | - | 10387-458430 | 70261 | - |
| | Open Sea | 5 | - | - | 4189-13206 | 8698 | - |
| 05.2009 | Open sea | 12 | - | - | 1514-26394 | 8542 | - |
| 06.2009 | Varna Bay | 5 | - | - | 20061-64433 | 47950 | - |
| | Open Sea | 12 | - | - | 4494-20851 | 10473 | - |
| 09.2009 | Varna Bay | 10 | 128-1985 | 1056 | 2008-11456 | 5263 | 20.1 |
| | Open Sea | 4 | 205-1405 | 806 | 4487-11216 | 7852 | 10.3 |
| 11.2009 | Varna Bay | 10 | 248-4492 | 1899 | 954-13289 | 6841 | 27.8 |
| | Open Sea | 4 | 368-1789 | 1016 | 1012-5962 | 3138 | 32.4 |
| 03.2010 | Varna Bay | 8 | - | - | 2913-25021 | 11040 | - |
| | Open Sea | 5 | - | - | 5910-7126 | 6518 | - |
| 04.2010 | Varna Bay | 10 | - | - | 7343-33730 | 16516 | - |
| | Open Sea | 5 | - | - | 5263-9462 | 7363 | - |
| 07.2010 | Varna Bay | 7 | 192-797 | 495 | 8133-18788 | 13461 | 3.7 |
| | Open Sea | 7 | 137-242 | 190 | 3850-9742 | 6796 | 2.8 |
| 08.2010 | Varna Bay | 7 | 1299-4921 | 2942 | 10091-31022 | 20557 | 14.3 |
| 09.2010 | Varna Bay | 7 | 6666-43818 | 19127 | 12399-53039 | 30111 | 63.5 |
| | Open Sea | 6 | 2321-11135 | 5988 | 4770-18249 | 11549 | 51.8 |
| 12.2010 | Open Sea | 5 | 19-549 | 203 | 112-3288 | 2079 | 9.8 |
| 04.2011 | Varna Bay | 7 | 87-93 | 90 | 5636-58571 | 34131 | 0.3 |
| 05.2011 | Varna Bay | 8 | 83-265 | 174 | 2152-13953 | 7892 | 2.2 |
| | Open Sea | 4 | 52-97 | 75 | 2342-13191 | 7139 | 1.1 |
| 07.2011 | Varna Bay | 6 | 141-304 | 223 | 6689-21272 | 16004 | 1.4 |
| | Open Sea | 11 | 59-341 | 151 | 2925-6856 | 5188 | 2.9 |
| 08.2011 | Varna Bay | 6 | 93-988 | 482 | 3536-9231 | 6322 | 7.6 |
| | Open Sea | 11 | 86-2172 | 691 | 652-21561 | 9980 | 6.9 |
| 09.2011 | Open Sea | 6 | 17-95 | 63 | 2411-7902 | 5202 | 1.2 |
| 10.2011 | Varna Bay | 6 | 2479-5918 | 3857 | 4121-17461 | 8714 | 44.3 |
| | Open Sea | 5 | 2065-3408 | 2737 | 2924-4842 | 3883 | 70.5 |
| 03.2012 | Bourgas Bay | 5 | 12-61 | 15 | 3708-23136 | 12576 | 0.1 |

63.5% and 70.5% recorded in September 2010 and October 2011 respectively (Table 1). Maximum density of *O. davisae* was documented in the Varna Bay in 2010, when only a month after the species' first appearance its abundance had increased 9-fold and reached ~ 3000 ind.m⁻³ in August. Later in September, the average abundance increased 6 fold with a maximum single-station estimate in the central part of the Bay of Varna of 43818 ind.m⁻³ (Table 1). The latter is slightly greater than a maximum density of 42667 ind.m⁻³ previously measured in Bay of Sevastopol (Gubanova and Altukhov 2007) and indicates comparable density ranges in different bay areas of the Black Sea.

For the two years (2010–2011) when there was consistent summer sampling, the abundance of O. davisae increased in August and sustained high levels in September 2010, but crashed to very low levels in September 2011 and then increased again in October 2011. In Crimea region, Gubanova and Altukhov (2007) observed an abundance increase of Oithona in September -October 2005. Obviously, in the Black Sea, the species proliferates in early autumn, but its abundance fluctuates widely from year to year and between the different months. The collected data show some differences with monthly pattern of population abundance of O. davisae in the native habitats. In the Japanese Sea for example, species' abundance begins increasing in spring, attains maximum levels by the middle of June, with quantities ranging from 50000 to 1×10^6 ind.m⁻³ (Hirota and Tanaka 1985; Uye and Sano 1998). The abundance remains high until mid July, then it declines to a mid-summer minimum, increases again in early September to form a fall peak, and finally declines until late winter (Uye and Sano 1998). Thus O. davisae could contribute to 99.8% of overall copepod abundance in Japanese waters (Hirota and Tanaka 1985; Uye and Sano 1998) while maximum contribution of O. davisae in the Black Sea is 92.6% of copepod abundance. However, direct comparison of abundance ranges between native habitats and the Black Sea is problematic because smaller mesh sizes were used for sample collection by Hirota and Tanaka (1985), and Uye and Sano (1998) provided a better estimation of the early, and more abundant, stages of the small oithonids. Temperature variation is comparable between the two localities, with a slightly higher temperature range in the Japanese Sea, 8.9-28.2°C (Uye and Sano 1998), while the Western Black Sea (WBS) ranged between $5.6-24.8^{\circ}$ C. Salinity is considerably higher in the Japanese Sea, 28.6 - 32.2 (Uye and Sano 1998) compared to the WBS at 15.8-17.2. Ferrari and Orsi (1984) described the presence of *O. davisae* in the Sacramento-San Joaquin Estuary (California, USA) in waters of salinities down to 12; hence, it is worth noting that *O. davisae* could well adjust to the brackish conditions in the Black Sea.

Extreme environmental conditions occurred in the Western Black Sea in summer 2010, before O. davisae reached maximal abundance. Higher than average air temperatures were observed in the spring and summer according to the meteorological data from the Varna weather station (Truhchev et al. 2010). Elevated temperatures were accompanied by low atmospheric dynamics, which reduced the water exchange between coastal and open-sea regions. In late August this led to the highest sea water temperatures (31.0°C and 31.5°C along the northern coasts) being registered in the history of meteorological investigations (Truhchev et al. 2010). In the bibliography it is well documented that the specific growth rate of the nauplia and copepodite stages of O. davisae increases exponentially with temperature (Uye and Sano 1998), and the period of egg development is also temperature-dependent (Uye and Sano 1995), thus contributing to enhanced concentrations of the species during warmer seasons. Calm weather could also play a role for swarms of O. davisae in early autumn of 2010, because the species appears sensitive to high and moderate turbulence intensities that might affect feeding capture success (Saiz et al. 2003).

Recent phytoplankton studies in the Black Sea have shown important structural changes and a prevalence of small flagellate species, explained mainly by climate-driven effects and reduced concentrations of nutrients (Nesterova et al. 2008; Mavrodieva 2012). O. daviase is a raptorial feeder, feeding on flagellates, dinoflagellates and ologotrichines (Uchima and Hirano 1986; Uchima 1988; Kiorboe and Viesser 1999; Saiz et al. 2003). Growth in the different developmental stages of the species could be restricted if the amount of food available becomes limited (Uchima and Hirano 1986; Almeda et al. 2010). Oithona nauplii. however, display lower metabolic rate and consequently lower food requirements than calanoid nauplii, which contributes to the ubiquity of the *Oithona* species

in marine ecosystems (Almeda et al. 2010). Castellani et al. (2007) found that the biomass of Oithona spp. varies significantly with temperature dinoflagellate and biomass concentration. Therefore, the current plankton community shift in the Black Sea associated with flagellate development may be small а significant driving force contributing to the proliferation of the O. davisae population, especially in the eutrophic inlets.

A reduction in the biomass of M. leidyi to levels below 1 g.m⁻² in September 2010 could also favor oithonid population growth. Since 2005, the quantity of *M. leidyi* in the Western Black Sea began to diminish notably due to an increased abundance of its introduced predator, the cteno-phore Beroe ovata; and abundance of prey species simultaneously increased its (Mihneva and Stefanova 2011). At present, the zooplankton in the eutrophic embayments has a low species diversity, dominated by the copepod Acartia clausi, the protozoa Noctiluca scintillans meroplankton larvae (Mihneva and and Stefanova 2011). It appears that O. davisae now occupies a niche in the shallow coastal waters during the warm months, where just a few years ago the zooplankton was heavily consumed by M. leidyi.

Plankton community evolution, under the increasing presence of O. davisae, may involve several "scenarios" (keeping in mind observations from other oceanic regions of the world where oithonids are already present in huge abundances). Because of the specific features of O. davisae, feeding on flagellates and not on diatoms and detritus, their mass development could affect the abundance of flagellates and bacteria (Roff et al. 1995). It is known that per capita herbivory of microzooplankton exceeds that of copepods (Burkill et al. 1993). Nakamura and Turner (1997) described some oithonids as "retrievers" of primary production by feeding on micro-zooplankton. Another important, yet open question for the Black Sea is whether the mass development of O. davisae will support fish or jellyfish populations. Recent observations show an enhanced abundance of the medusae Aurelia aurita alongside diminishing populations of M. leidyi and an improved mesozooplankton food base. However, a stable increasing trend in fish species' abundances has not yet been observed in the region (Oguz et al. 2012).

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References

- Almeda R, Augustin C, Alcaraz M, Calbet A, Saiz E (2010) Feeding rates and gross growth efficiencies of larval developmental stages of *Oithona davisae* (Copepoda, Cyclopoida). *Journal of Experimental Marine Biology and Ecology* 387(1–2): 24–35, http://dx.doi.org/10.1016/j.jembe. 2010.03.002
- Burkill P, Edwards J, John A, Sleigh M (1993) Microzooplankton and their herbivorous activity in the north-eastern Atlantic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 40(1-2): 479-493, http://dx.doi.org/10.1016/ 0967-0645(93)90028-L
- Calbert A, Agusti S (1999) Latitudinal changes of copepod egg production rates in Atlantic waters: temperature and food availability as the main driving factors. *Marine Ecology Progress Series* 181: 155–162, http://dx.doi.org/10.3354/ meps181155
- Castellani C, Irigoien X, Harris R, Holliday N (2007) Regional and temporal variation of *Oithona* spp. biomass, stage structure and productivity in the Irminger Sea, North Atlantic. *Journal of Plankton Research* 29(12): 1051–1070, http://dx.doi.org/10.1093/plankt/fbm079
- Ferrari F, Orsi J (1984) Oithona davisae, new species, and Limnoithona sinensis (Burkckhard, 1912) (Copepoda: Oithonidae) from the Sacramento-San Joaquin Estuary, California. Journal of Crustacean Biology 4(1): 106–126, http://dx.doi.org/10.2307/1547900
- Gallienne CP, Robin DB (2001) Is *Oithona* the most important copepod in the world's oceans? *Journal of Plankton Research* 23(12):1421–1432, http://dx.doi.org/10.1093/plankt/23.12.1421
- Gubanova A, Altukhov D (2007) Establishment of Oithona brevicornis Giesbrecht, 1892 (Copepoda: Cyclopoida) in the Black Sea. Aquatic Invasions 2: 407–410, http://dx.doi.org/ 10.3391/ai.2007.2.4.10
- HELCOM Annex C 7: http://www.helcom.fi/groups/monas/ CombineManual/AnnexesC/en_GB/annex7/?u4.highlight=zoopl ankton (Accessed 30 January 2013)
- Hirota R, Tanaka Y (1985) High abundance of Oithona davisae (Copepoda, Cyclopoida) in the shallow waters adjacent to the mud flats in Ariake-kai, western Kyushu. Bulletin Plankton Society Japan 32: 169–170
- Kiorboe T, Visser A (1999) Predator and prey perception in copepods due to hydromechanical signals. Marine Ecology Progress Series 179: 81–95, http://dx.doi.org/10.3354/meps 179081
- Konsulov A, Kamburska L (1998) Ecological determination of the new ctenophore - *Beroe ovata* invasion in the Black Sea. *Okeanologia (Oceanology)*, Bulgarian Academy of Science, 2, pp 195–198

- Korshenko A, Aleksandrov B (2006) Manual for mesozooplankton sampling and analysis in the Black Sea Region, Black Sea Commission, 36 pp
- Kideys A, Romanova Z (2001) Distribution of gelatinous macroplankton in the southern Black Sea during 1996–1999. *Marine Biology* 139: 535–547, http://dx.doi.org/10.1007/s00 2270100602
- Nakamura Y, Turner J (1997) Predation and respiration by the small cyclopoid copepod Oithona similis: How important is feeding on ciliates and heterotrophic flagellates? Journal of Plankton Research 19: 1275–1288, http://dx.doi.org/10.1093/ plankt/19.9.1275
- Nesterova D, Moncheva S, Mikaelyan A, Vershinin A, Akaktov V, Boicenco L, Akatan Y, Sahin F, Gvarishvili T (2008) The state of phytoplankton. In: Oguz T (ed), State of the environment of the Black Sea (2001–2006/7). The Commission on the Protection of the Black Sea against Pollution publication, Istanbul, pp 173–200
- Mavrodieva R (2012) Mechanisms of interactions between phytoplankton and marine environmental factors (biotic and abiotic) in the Bulgarian Black Sea coastal waters (Sozopol Bay). PHD thesis, Institute of Biodiveristy and Ecosystem Research (Bulgarian Academy of Science), Sofia, 193 pp
- Mihneva V, Stefanova K (2011) Species diversity and dynamics of zooplankton abundance and biomass off the Bulgarian Black Sea coast in 2008–2010, Proceedings of the Union of Scientists – Varna'2011, pp 97–104
- Oguz T, Akoglu E, Salihoglu B (2012) Current state of overfishing and its regional differences in the Black Sea. Ocean & Coastal Management 58: 47–56, http://dx.doi.org/ 10.1016/j.ocecoaman.2011.12.013
- Pereladov M (1988) Some observations on the biological community changes in the Sudak Bay (Black Sea). Thesis III All Russia Union Conference on Marine Biology. Sevastopol, Kiev, pp 237–238
- Roff J, Turner T, Webber K, Hopcroft R (1995) Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquatic Microbial Ecology* 09(2): 165–175, http://dx.doi.org/ 10.3354/ame009165
- Razouls C, de Bovee F, Kouenberg J, Desreumaux N (2012) Diversity and Geographic Distribution of Marine Planktonic Copepods: http://copepodes.obs-banyuls.fr/en/fichesp.php?sp= 1776 (Accessed 30 January 2013)
- Saiz E, Calbet A, Broglio E, Marı P (2003) Effects of small-scale turbulence on copepods: The case of *Oithona davisae*. *Limnology and Oceanography* 48(3): 1304–1311, http://dx.doi.org/10.4319/lo.2003.48.3.1304
- Selifonova Zh (2009) *Oithona brevicornis* Giesbrecht (Copepoda, Cyclopoida) in Harborages of the Northeastern Part of the Black Sea Shelf. *Inland Water Biology* 2(1): 30–32

Schlitzer R (2011) Ocean Data View, http://odv.awi.de

- Shiganova T (1997) Mnemiopsis leidyi abundance in the Black Sea and its impact on the pelagic community. Ozsoy & Mikaelyan (eds), Sensitivity to change: Black Sea, Baltic Sea and North Sea, pp 117–129
- Shushkina E, Nikolaeva G, Lukasheva T (1990) Changes in the structure of the plankton community in the Black Sea during the mass development of the ctenophore *Mnemiopsis leidyi* (Agassiz). *Jurnal Obstei Biologii (Journal of Common Biology*) 51(1): 54–60
- Temnykh A, Nishida Sh (2012) New record of the planktonic copepod Oithona davisae Ferrari and Orsi in the Black Sea with notes on the identity of "Oithona brevicornis". Aquatic Invasions 7: 425–431, http://dx.doi.org/10.3391/ai.2012.7.3.013
- Truhchev D, Shtereva G, Krastev A, Trayanov T (2010) Oceanographic investigations of the coastal sea area affected by Kamchiya river inflow. Proceedings of the Union of Scientists – Varna 2'2010, XV, pp 34–44
- Turner J (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zoological Studies* 43(2): 255–266
- Uchima M (1988) Gut content analysis of neritic copepods Acartia omorii and Oithona davisae by a new method. Marine Ecology Progress Series 48: 93–97, http://dx.doi.org/ 10.3354/meps048093
- Uchima M, Hirano R (1986) Food of *Oithona davisae* (Copepoda: Cyclopoida) and the effect of food concentration at first feeding on the larval growth. *Bulletin of the Plankton Society of Japan, Hiroshima* 33(1): 21–28
- Uye Sh, Sano K (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Marine Ecology Progress Series* 118: 121– 128, http://dx.doi.org/10.3354/meps118121
- Uye Sh, Sano K (1998) Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Marine Ecology Progress Series* 163: 37–44, http://dx.doi.org/10.33 54/meps163037
- Vinogradov ME (1989) The vertical zonality of the Black Sea pelagic ecosystem. Doklady Akademii Nauk Souz Sovetskih Respublik (Reports of the Academy of Science of Soviet Union) 306(3): 717–721
- Zagorodnyaya Yu (2002) *Oithona brevicornis* in the Sevastopol Bay: is it a single event or a new invader in the Black Sea fauna? *Morskoy Ekologicheskiy Jurnal (Marine Ecology Journal)* 61: 43
- Zaitsev Yu, Mamaev V (1997) Biological diversity in the Black Sea: a study of change and decline. UN Publications, New York, 228 pp