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INFLUENCE OF INVADER CTENOPHORES ON BIOLUMINESCENCE VARIABILITY OFF THE COAST OF WESTERN CRIMEA

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In the second half of the XX century, Black Sea ecosystem has undergone significant changes: a number of storm winds and upwellings decreased, precipitation abundance increased, coastal waters salinity decreased, temperature increased; moreover, ctenophores invaded. As a result, in the late 1980s, Black Sea pelagic ecosystem abruptly got restructured. This research is based on the studies performed in 1965–1966 and 2007–2012 near Sevastopol (Western Crimea) using the remote sensing data. Analysis of satellite data over the past 20 years showed the presence of positive dynamics in surface water temperature in Sevastopol water area. In the mid-1960s, the annual bioluminescence was characterized by seasonal peaks of dinophytes luminescence. In recent years, this rhythm has changed due to ctenophores invasion. The increase in *Mnemiopsis leidyi* abundance leads to a decrease in bioluminescence of luminous microalgae being consumed by these ctenophores. Due to *Beroe ovata* invasion and reproduction, *M. leidyi* biomass decreased; as a result, bioluminescence increased.

Keywords: Black Sea, bioluminescence, ctenophores, salinity, monitoring

Biophysical studies in the Black Sea began in the 1960s when D. Sc. E. Bityukov (IBSS) made the first annual measurements of bioluminescence in Sevastopol area [2]. Thus, in 1965–1966, 18 expeditions were carried out for instrumental measurements, and 72 net samplings of plankton were taken. Continuation of these works was initiated by D. Sc. Yu. Tokarev (IBSS); the studies were carried out in 2008–2015. So, it became possible to evaluate the long-term changes of coastal water bioluminescence under conditions of climate changes.

The climate changes in Black Sea ecosystem have led to the invasion of huge number of new luminous species: they were brought in with ballast waters from other regions. Therefore, all past experience and knowledge about Black Sea bioluminescence are subject to minor adjustments.

Before ctenophores invasion, bioluminescence field in Black Sea photic layer was formed by luminous dinoflagellates [4]. In the early 1980s, ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 invaded the Black Sea, which led to a significant reduction in plankton base and fish food [18]. In the late 1990s, another ctenophore, *Beroe ovata* Mayer, 1912, invaded the Black Sea and began to consume *Mnemiopsis leidyi* [6]. Now, the system is balanced: when the number of one species increases, the number of other species decreases. Therefore, it was suggested that these invader species should make a significant contribution to changing the seasonal dynamics of coastal water bioluminescence.

The aim of this work is to determine influence of these two species on the seasonal dynamics of coastal water bioluminescence.

MATERIAL AND METHODS

The fieldwork was carried out at the 10-mile station off the Kruglaya Bay (No. 1) and at two stations in the Sevastopol Bay (No. 2 and 3) (Western Crimea) (Fig. 1). The research was based on the real-time instrumental measurements of bioluminescence amplitude-frequency parameters, as well as on the determination of their spatial conjugacy with biological and hydrophysical characteristics of water masses.

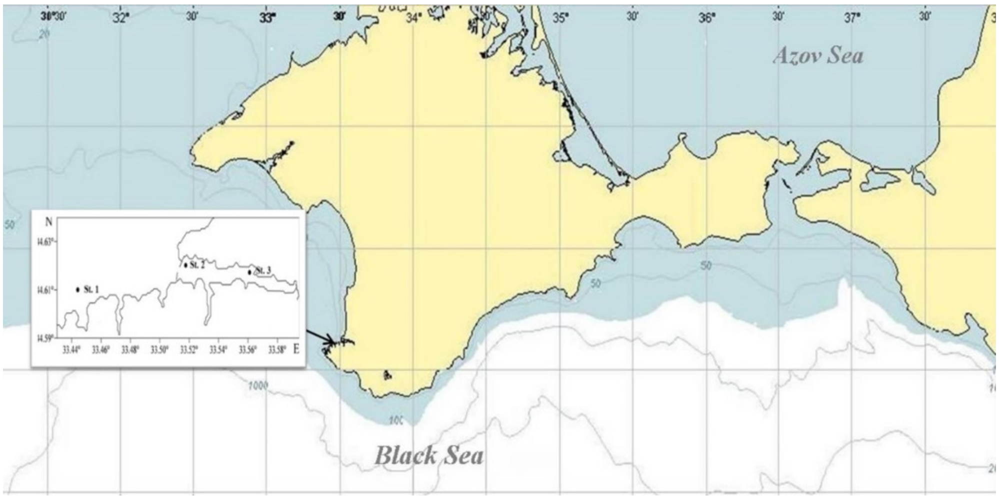

Fig. 1. Map of stations

Station No. 1, located near the Kruglaya Bay (depth of 60 m), has water exchange with the open sea and is characterized by a fairly stable stratification of water column, which determines the vertical structure of temperature and salinity. Stations No. 2 and 3 are located in the Sevastopol Bay, and water exchange with the open sea is limited. In addition, the Sevastopol Bay includes the mouth of the Chernaya River, which is the flow of fresh water into the bay; this results in mixing of river water and seawater [15]. Depending on the volume of river flow, the impact of fresh water extends to different zones of the bay, which significantly affects region ecological conditions. Water area of Konstantinovskaya Bay (station No. 2, depth of 19 m) is relatively clean. Gollandiya Bay (station No. 3, depth of 18 m) is located in the central part of the Sevastopol Bay in the zone of active mixing of river water and seawater [8].

Bioluminescence intensity and background parameters were recorded using a submersible complex "Salpa-M" [21]. It allows taking simultaneous measurements of bioluminescent potential, temperature, hydrostatic pressure, turbidity, and photosynthetically active radiation. "Salpa-M" has four rows of blackened impellers, consisting of two groups of rows mutually perpendicular to attack angles and forming a moving light trap. This ensures the attenuation of light energy by $2 \cdot 10^7$ times, which is especially important during the daytime. The weight of the submersible complex does not exceed 15 kg; it is designed for autonomous power supply of 24 V.

Discreteness of the measurements during the "down" operation at a speed of 1.2 $m \cdot s^{-1}$ was about 0.25 m. To construct graphs of vertical profiles, the data were integrated up to 1 m. The method of collecting and processing the data using the "Salpa-M" complex was previously described in details [21]. On processing its data, profiles of bioluminescence, temperature, salinity, and conditional density of water were calculated. Results of the measurements were processed and added to a database [13].

Simultaneously with measurements with the "Salpa-M" complex, phytoplankton samples were taken using a bathometer. The fieldwork was carried out both at night (the period of maximum bioluminescence) and at daytime (the period of minimum bioluminescence). At each station, measurement with the "Salpa-M" complex was carried out twice. During several cruises of RV "Professor Vodyanitsky", 10 to 30 continuous soundings were made by the "Salpa-M" complex at station No. 1.

Changes in sea surface temperature (hereinafter SST) in Sevastopol area were analyzed for 2008–2017 based on the analysis of remote sensing data. Under the conditions of a sea expedition, methodological approaches described in this article were tested, which will be applied in the scientific researches in the Antarctic region.

RESULTS

Mean annual SST values (°C) have a negative trend since 1982 reaching its minimum in 1987; then, the period until 2017 is characterized by a significant positive trend (Fig. 2). Since trend lines were constructed by least squares calculation, the accuracy of the approximation was estimated by the coefficient of determination. This graph clearly shows that during the period of ctenophores invasion in the area studied, substantial warming of surface waters occurred.

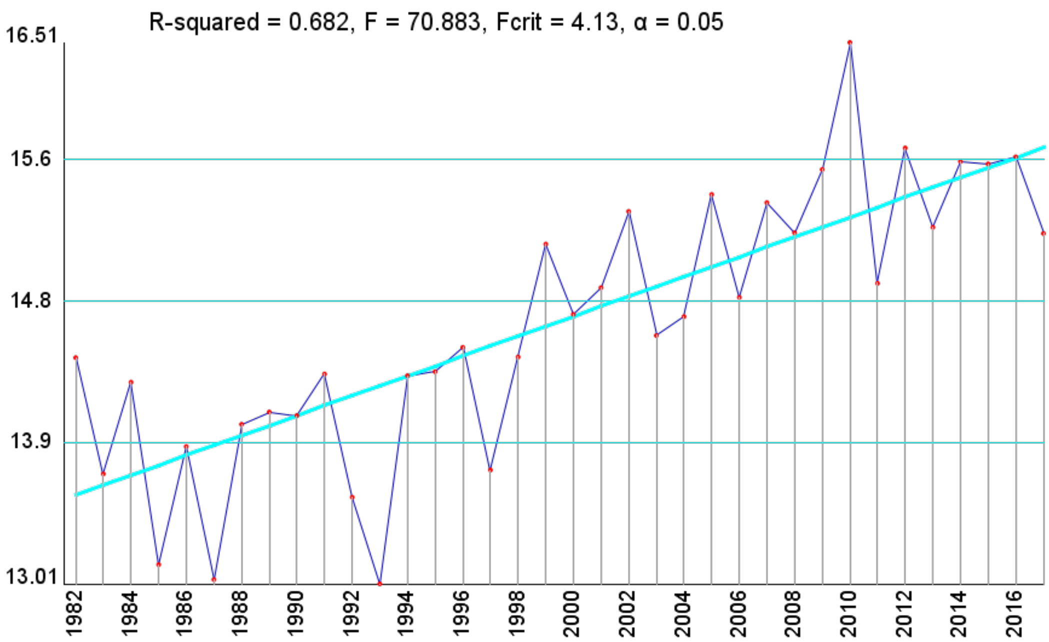

Fig. 2. Mean annual sea surface temperature values (°C) calculated for 1982–2017 with a spatial resolution of 0.0417° in latitude and longitude. *R*-squared (R^2) is the coefficient of determination; *F* is Fisher's *F*-test; *Fcrit* is the critical value of Fisher's *F*-test for the data considered at the accepted confidence probability α [14]

Data analysis showed that in 1965–1966, two seasonal peaks of bioluminescence were observed (Fig. 3A), which were associated with spring and autumn phytoplankton blooming [5]. In recent years, global warming has changed this rhythm. Thus, in 2008–2012, the seasonal dynamics of bioluminescence on Sevastopol coast was characterized by the appearance of additional peaks in the warm season, associated with the outbreaks of warm-water invader ctenophores – *M. leidyi* and *B. ovata* (Fig. 3A). Under favorable conditions, abrupt outbreaks of *B. ovata* abundance are possible, often alternating with recessions up to its complete disappearance (this, for example, is typical of North America coast [11]). It resulted in significant imbalance in the seasonal dynamics of the coastal water bioluminescence near Sevastopol.

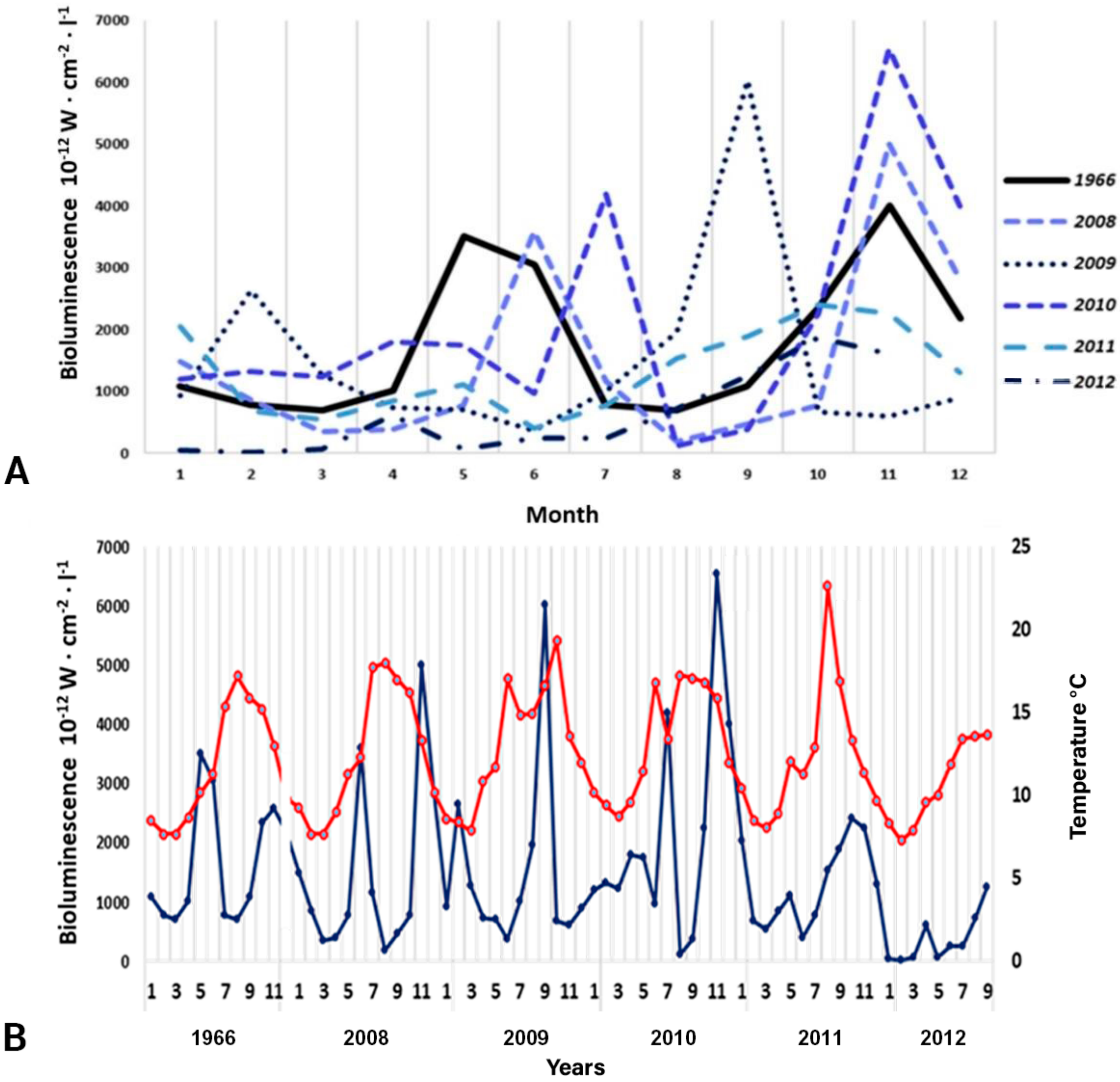

Fig. 3. A – seasonal dynamics of bioluminescence intensity; B – inter-annual dynamics of bioluminescence (mean values are indicated by a blue line) and water temperature (red line) in Sevastopol coastal waters in 55-m layer (1966, 2008–2012)

The inter-annual dynamics of temperature and bioluminescence (Fig. 3B, Table 1) was characterized by the presence of a positive annual mean trend – an increase in mean values of water temperature in 0–55-m layer from +12.11 °C (2008) to +12.89 °C (2010). The maximum summer values of the mean temperature increased from +18.00 °C (August 2008) to +22.62 °C (August 2011).

The peaks of bioluminescence (Fig. 3B) were observed in June 2008 ($3594 \cdot 10^{-12}$ $W \cdot cm^{-2} \cdot L^{-1}$), in July 2009 ($4200 \cdot 10^{-12}$ $W \cdot cm^{-2} \cdot L^{-1}$), and in September 2009 ($6029 \cdot 10^{-12}$ $W \cdot cm^{-2} \cdot L^{-1}$), as well as in spring and autumn regularly due to phytoplankton blooming (Table 1).

The vertical structure of bioluminescence in all the seasons was determined by hydrological conditions, especially thermocline layer location. Bioluminescence is mainly represented by a structure of two maxima separated by a water column where bioluminescence is reduced. The upper stationary layer was almost always observed at a depth of 0–6 m; the lower layer with a higher luminosity migrated within 15–64 m and was located in thermocline area.

Table 1. Mean values of water temperature (T, °C) and bioluminescence (B, $\cdot 10^{-12}$ W$\cdot$cm$^{-2}\cdot$L^{-1}) at station No. 1 (I–XII indicate months January till December)

Year	1966		2008		2009		2010		2011		2012	
Index	T	B	T	B	T	B	T	B	T	B	T	B
I	8.5	1094	9.3		8.62	929	10.16	1204	10.45	2048	8.35	42
II	7.7	781	7.7	859	8.38	2643	9.42	1326	8.5	691	7.29	17
III	7.7	703	7.7	352	7.9	1274	8.72	1233	8.07	544	7.94	68
IV	8.7	1016	9.0	391	10.84	733	9.62	1801	8.92	850	9.58	618
V	10.2	3516	11.3	781	11.75	700	11.48	1754	12.04	1104	10.06	76
VI	11.3	3047	12.3	3594	17.03	371	16.81	974	11.27	412	11.88	249
VII	15.4	781	17.7	1172	14.9	1011	13.43	4200	12.89	772	13.46	248
VIII	17.2	703	18.0	195	14.91	1970	17.24	126	22.62	1534		
IX	15.9	1094	17.0	469	16.62	6029	17.07	386	16.92	1898	13.71	1254
X	15.2	2344	16.2	781	19.36	675	16.81	2257	13.30	2410		
XI	13.0	2574	13.3	5000	13.57	608	15.87	6545	11.37	2256		
XII	9.8	2188	10.2	2813	12.00	900	12.00	4000	9.70	1304		

Studies of the inter-annual dynamics of invader ctenophores abundance near Sevastopol in 2009–2010 [1] showed that seasonal peaks for *M. leidyi* and *B. ovata* do not coincide (Fig. 3) due to differences in diets of these species. Increase in *B. ovata* abundance leads to decrease in *M. leidyi* abundance, which restores the number of luminous dinoflagellates. Recently it has been found out [20] that even *M. leidyi* larvae and post-larvae are likely to consume significant amounts of microphyto- and zooplankton including dinoflagellates, ciliated infusoria, and other flagellates.

B. ovata is the main consumer of *M. leidyi* in the Black Sea. Peaks of its seasonal abundance occur at the end of summer, when *M. leidyi* biomass reaches its maximum value. After density of food resource reduces, *Beroe* populations continue to persist due to a decrease in the mean body size of individuals [12].

Using the statistical analysis (Pearson's correlation coefficient, r) on the data on invader ctenophore abundance and bioluminescence dynamics showed that correlation between *M. leidyi* traits studied and the bioluminescence is low (–0.49) (Figs 4, 5). Correlation between *B. ovata* traits studied and the bioluminescence was assessed as strong (0.71). It can be concluded that in cases of $r = -0.49$, the increase in *M. leidyi* biomass moderately affects the decrease in bioluminescence intensity. In cases of $r = 0.71$, the increase in *B. ovata* biomass significantly affects the increase in bioluminescence intensity. Correlation between these data was measured by the Chaddock scale. Criteria for evaluation were as follows: $0.1 < r < 0.3$ (weak); $0.3 < r < 0.5$ (moderate); $0.5 < r < 0.7$ (noticeable); $0.7 < r < 0.9$ (strong); $0.9 < r < 1$ (very strong).

DISCUSSION

Because of the global warming, intensive distribution and development of gelatinous plankton has occurred in various marine areas of the world in recent decades. Significant secular trends of increasing air temperature (by 0.4–0.8 °C per 100 years) are observed along Black Sea coast, which corresponds to global warming estimates [9]. During the second half of the XX century, the recurrence of strong winds and upwellings decreased three times; a significant increase in precipitation and a decrease in evaporation were observed [10 ; 14]. This created the conditions for the resettlement of invader species, which have radically changed Black Sea ecosystem.

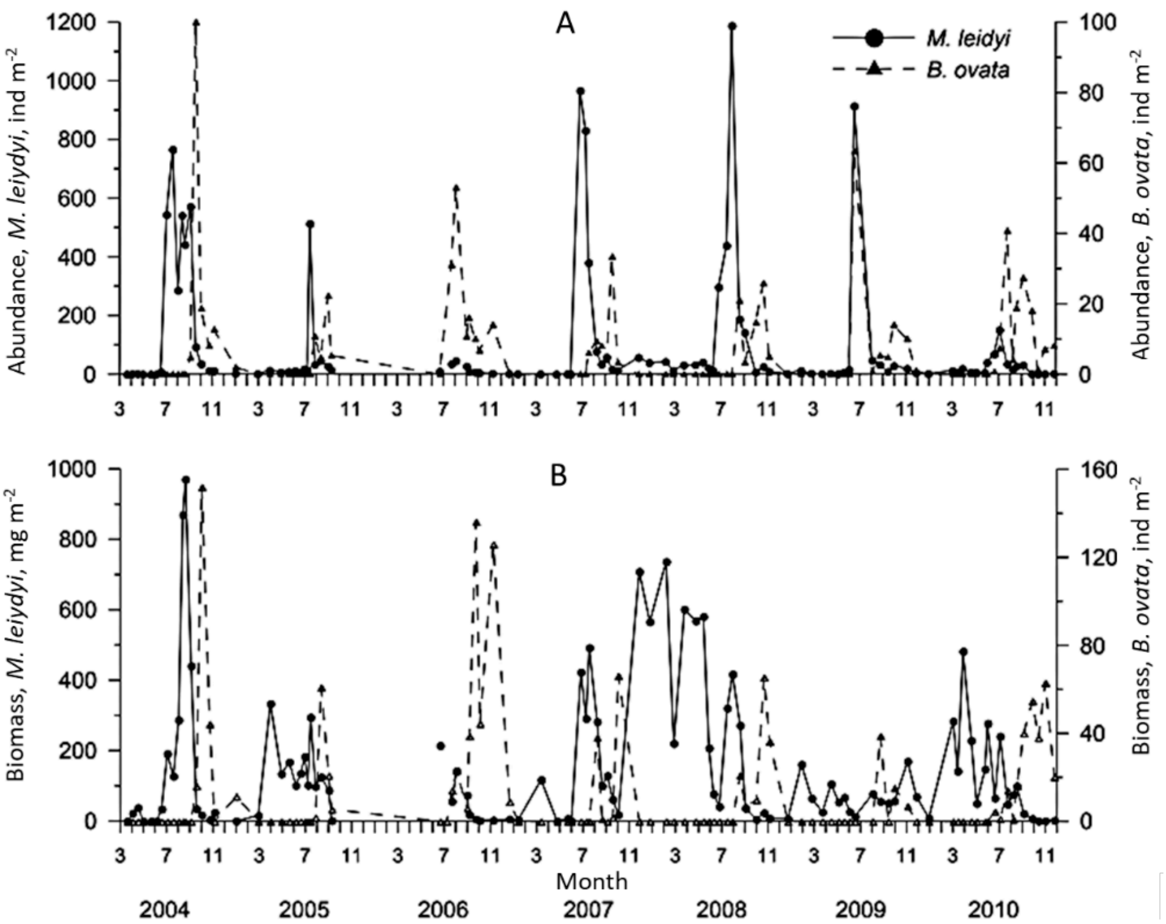

Fig. 4. Inter-annual dynamics of *Mnemiopsis leidyi* and *Beroe ovata* abundance (A) and biomass (B) [1]

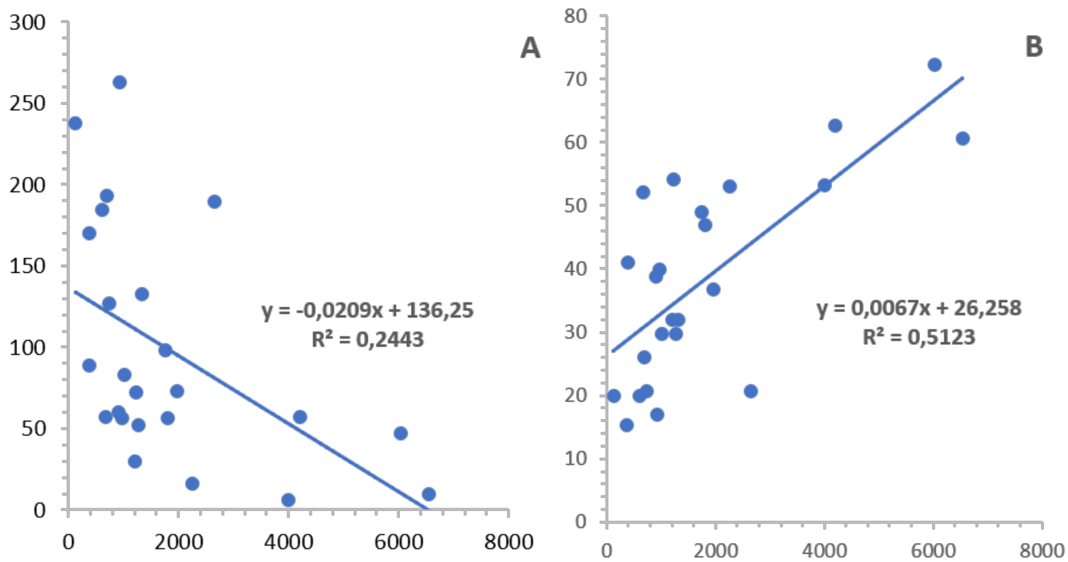

Fig. 5. Dependence of bioluminescence on ctenophores biomass: A – *Mnemiopsis leidyi*; B – *Beroe ovata* (for 0–10-m layer)

In the Black Sea, warm-water ctenophores appeared about 40 years ago [17 ; 18], as well as in the Sea of Azov [12] and the Caspian Sea [19]. Everywhere, *M. leidyi* invasion led to catastrophic changes in marine ecosystems [23]. For a decade, due to the absence of natural predators, *M. leidyi* development in the Black Sea was controlled only by temperature and food availability [7]. In 1997, its consumer, new carnivorous ctenophore *B. ovata*, was firstly discovered in the Black Sea; in 1999 and 2000, *Mnemiopsis* population density began to decline rapidly due to *Beroe* mass development [22]. Before the invasion of this predatory ctenophore, *Mnemiopsis* had abundance peaks in warm season. Now, in the summertime, the second minimum of its abundance is formed, due to *B. ovata* intensive development.

Till now, there are practically no studies on the effect of these invaders on the overall variability of Black Sea bioluminescence. Prior to their invasion, the total luminosity of coastal waters was determined by seasonal peaks of dinoflagellates development [2 ; 3 ; 4 ; 5]. Invader ctenophores do not only actively luminesce on their own, but also have a decisive influence on species composition and abundance of other bioluminescents.

According to the results of the detailed study of the long-term variability of bioluminescence in 2009–2012 in the research area [16], seawater luminescence in winter occurs due to the development of microalgae *Ceratium fusus* Ehrenb., *C. tripos* Ehrenb., *C. furca* Ehrenb., *Protoperidinium divergens* (Ehrenb.) Balech, *P. crassipes* (Kof.) Balech, *P. pallidum* (Ostenf.) Balech, *P. depressum* (Bailey), and *Balech oblongum* (Auriv.) Parke & J. D. Dodge. The second peak of the development of microalgae, Gonyaulax, *Scrippsiella trochoidea* (F. Stein), *Scrippsiella* Balech ex A. R. Loeblich III, 1965, and *Lingulodinium polyedrum* (F. Stein) J. D. Dodge, was observed during the springtime. This study has shown that the seasonal variability of total bioluminescence occurs in spring and autumn till now, as it was observed in the 1970s. Meanwhile, now bioluminescence peaks are sometimes twice as high as they were 50 years ago. It is likely that, in addition to microalgae contribution, in certain seasons of the year, the total area of luminous water increases due to ctenophores bioluminescence contribution. The authors of the present study very often register rapid increases of bioluminescence level in areas of ctenophores swarms in Sevastopol coastal waters. However, the incompleteness of these data does not allow one to estimate direct ctenophores contribution to the total water luminosity. On the other hand, ctenophores abundance is not comparable with that of phytoplankton determining the total bioluminescence of coastal waters.

Thus, the results of this study showed that differences in food modes of ctenophores have a significant impact on the seasonal dynamics of the bioluminescence of Black Sea coastal waters. The invasion of a new predatory species has led to the emergence of a balance, that depends on the nature of regional climatic and seasonal changes in the aquatic environment.

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ВЛИЯНИЕ ГРЕБНЕВИКОВ-ВСЕЛЕНЦЕВ НА ИЗМЕНЧИВОСТЬ БИОЛЮМИНЕСЦЕНЦИИ У БЕРЕГОВ ЗАПАДНОГО КРЫМА

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Во второй половине XX века произошли значительные изменения в экосистеме Чёрного моря. Так, число штормовых ветров и апвеллингов уменьшилось, осадки стали обильнее, солёность прибрежных вод снизилась, температура водных масс повысилась. Кроме того, произошло вселение гребневиков. В итоге в конце 1980-х гг. пелагическая экосистема Чёрного моря резко перестроилась. Данная работа основана на исследованиях, выполненных при помощи дистанционного зондирования в 1965–1966 и 2007–2012 гг. в районе г. Севастополя (Западный Крым). Анализ спутниковых данных за последние 20 лет показал наличие положительной динамики температуры поверхностных вод в акватории Севастополя. В середине 1960-х гг. годовая динамика биолюминесценции характеризовалась сезонными пиками свечения динофитовых микроводорослей. В последние годы этот ритм изменился из-за вселения гребневиков. Увеличение численности *Mnemiopsis leidyi* приводит к уменьшению биолюминесценции светящихся микроводорослей, которых этот гребневик потребляет. Вселение и размножение *Beroe ovata* обусловило резкое уменьшение биомассы *M. leidyi* и, как следствие, рост биолюминесценции.

Ключевые слова: Чёрное море, биолюминесценция, гребневик, солёность, мониторинг