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COMPARISON OF POPULATION PARAMETERS OF THE INDIAN OIL SARDINE *SARDINELLA LONGICEPS* FROM THE MUSCAT REGION (SULTANATE OF OMAN) IN 1997 AND 2020–2021

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The Indian oil sardine *Sardinella longiceps* plays a key role in the coastal ecosystem of Oman and its fisheries. Total sardine landings along the Omani coast have increased dramatically: from approximately 17,000 t in 1997 to 440,000 t in 2021. A comparison of *S. longiceps* size structure, length–weight relationship, maturity, spawning seasons, growth, mortality parameters, and some stock characteristics in 1997 and in 2020–2021, as well as data obtained during earlier studies in Oman, shows that the biological structure of the population has been relatively stable over the time. The exploitation rate was higher than 0.5, and although the Indian oil sardine can sustain high exploitation rates, its stock in the Omani waters was overexploited. The biological data acquired during the present study provide a basis for management of the fishery; however, monitoring of catches should be continued, so that a longer time series of biological information can be collected and analyzed.

Keywords: Indian oil sardine, *Sardinella longiceps*, length composition, reproductive characteristics, growth, mortality, stock, long-term changes, Muscat, Sea of Oman

Fisheries play a vital role in coastal communities contributing significantly to employment, food security, nutrition, and national economy of the Sultanate of Oman. According to fisheries statistics of FAO [2024], the total fish catches in Oman rose from about 118,600 metric tons (t) in 1994 to 922,000 t in 2021 (Fig. 1A). This remarkable growth was mainly due to increased catches of sardines by almost 27 times, from 14,100 t in 2008 to 376,000 t in 2021, in two regions, Al Wusta and Al Sharqiyah [Fisheries Statistics Book, 2013, 2022]. In other regions, the changes of the sardine landings were not as noticeable. For example, in the Muscat region, the mean landing of sardines during 1994–2011 was around 10,000 t and decreased to only 3,200 t during 2012–2022 [Fisheries Statistics Book, 2003, 2013, 2022] (Fig. 1B). Overall, sardine landings contributed to about 24% of total fishery production in Oman in 1994–2011, and their share increased to approximately 50% in 2018–2021. Recently, the total sardine landing in Oman has dropped significantly, from 440,156 t in 2021 to 280,623 t in 2022. In the Muscat region, the landing has also decreased, from 5,404 t to 3,906 t during these years.

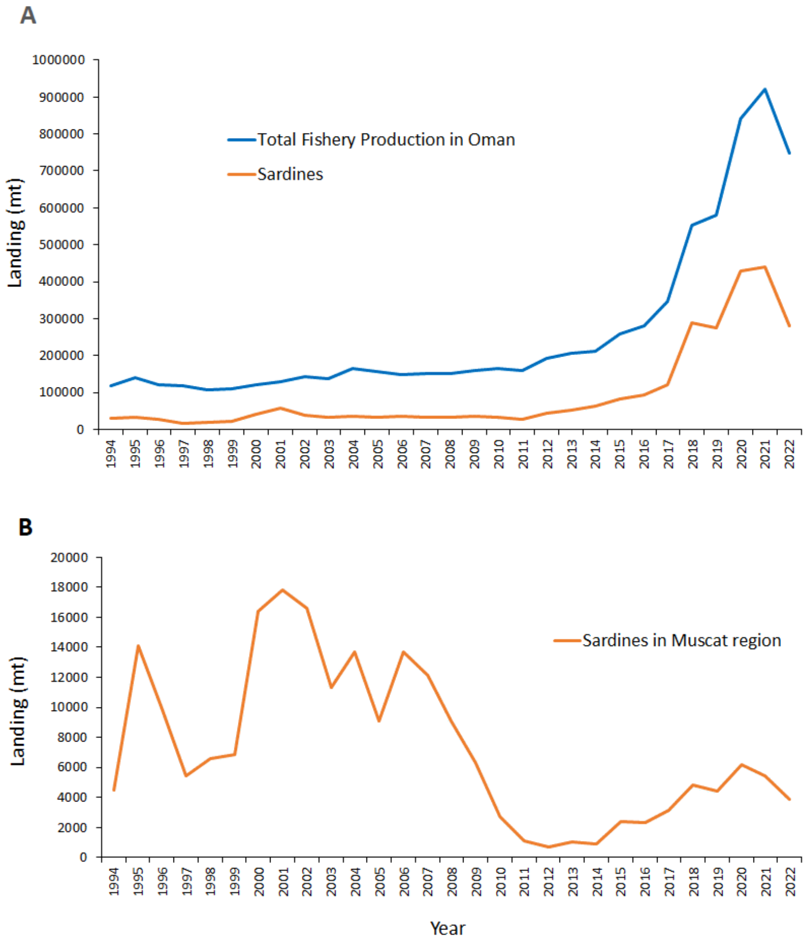

Fig. 1. Total fishery production and sardine landings in Oman (A) and total catches of sardines in the Muscat region (B) in 1994–2022

Five species of sardines (*Sardinella albella*, *S. gibbosa*, *S. longiceps*, *S. melanura*, and *S. sindensis*) are reported from the Omani waters [FishBase, 2024; Randall, 1995]. However, in addition to these species, the blue stripe herring (*Herklotsichthys quadrimaculatus*) and gizzard shad (*Nematalosa nasus*) have been included in the statistics of sardine landings in Oman in recent years [Fisheries Statistics Book, 2013, 2020, 2022]. According to [Al Jufaili, 2021; Al-Abdessalaam, 1995; Zaki et al., 2021], the Indian oil sardine *Sardinella longiceps* Valenciennes, 1847 contributes to about 80% of the total sardine catches in Oman; therefore, this species is of particular interest.

The biology of the Indian oil sardine from different areas of Oman was first studied by M. Al-Barwani *et al.* [1989]. Research by J. Shaklee and M. Shaklee [1990] suggested the presence of a unit stock of *S. longiceps* in the Omani waters. Different aspects of the reproduction biology of this species have been described by M. Siddeek *et al.* [1994], S. Al Jufaili [2011] S. Al Jufaili *et al.* [2006], I. Al-Anbouri *et al.* [2013], and S. Zaki *et al.* [2021]. A comprehensive study on the fishery, biology, and stock assessment of the Indian oil sardine was undertaken along the Omani coast during 2007–2009 under the “Small Pelagic Fisheries Project” [Zaki et al., 2011]. Age, growth, mortality, and some stock parameters have been investigated in various regions of Oman, including Muscat [Al-Anbouri et al., 2011; Zaki et al., 2011], Salalah [Zaki et al., 2011, 2013a], Sohar [Zaki et al., 2011, 2013b], and Mahout [Jayabalan et al., 2014; Zaki et al., 2011]. Several articles were published on *S. longiceps* fishery in Oman, *inter alia* those covering studies on gillnet selectivity [Govender, Al-Oufi, 2020], factors driving seasonal and interannual fluctuations of sardine catches [Al Jufaili, Piontkovski, 2020; Piontkovski et al., 2014], and changes in sardine landings along different regions of the Omani coast in 1995–2020 [Al Jufaili, 2021]. Recently, S. Dutta *et al.* [2021; 2024] estimated some population parameters of *S. longiceps* based on samples from the Muscat region in 1997 and between 2004 and 2009. The research of S. Dutta *et al.* [2024] showed that the stock of the species was largely overexploited during these years, with the exception of 2007. Dramatic fluctuations in the Indian oil sardine catches not only lead to changes in income from its fishery, but also affect other valuable marine species, because the sardine is the primary food source for a variety of large pelagic fish, marine mammals, and birds.

The main aim of the study was to compare population parameters of *Sardinella longiceps* in the Muscat region between 1997 and 2020–2021 to determine whether there have been any changes in the biological structure of its assumed single unit stock due to an increase in its total catch in Oman by almost 27 times, although this rise occurred in other areas.

MATERIAL AND METHODS

S. longiceps was sampled randomly in Seeb fish market (the Muscat region) on a monthly basis January to December 1997 (1,375 specimens) and during the period October 2020 to August 2021, except July (394 specimens). The fish were caught by traditional artisanal fishermen using gillnets, surrounding nets, and cast nets. The fish were transferred to the laboratory of the Sultan Qaboos University and measured in total length (TL) to the nearest 1 mm. The total weight (W) and gonad weight (GW) were recorded to the nearest 0.01 g using an electronic balance (Mettler PE 360). Sex and stage of gonad maturity were identified by visual observation of gonads using the five maturity stages scale based on size and color appearance of gonads [Al-Anbouri et al., 2011; Fisheries Techniques, 1995].

The length–weight relationship was estimated using the allometric formula [Le Cren, 1951]:

$$W = a \times L^b \,, \tag{1}$$

where W is the total wet weight (g);

L is the total length (cm);

a and b are the constants.

The values of the constants a and b were estimated by the least-square linear regression from the logarithmic transformation values of length and weight:

$$\log W = \log a + b \log L \,, \tag{2}$$

where b is the slope;

log a is the intercept [Zar, 1999].

The regression analysis was conducted using the Regression Analysis tool in MS Office Excel. The 95% confidence limits (*CL*) of parameters a and b and coefficient of determination (Pearson r^2) were estimated. The coefficient of determination was used as an indicator of the linear regression quality. Regressions were calculated for males, females, and both sexes combined. Analysis of covariance (ANCOVA) was used to find out the significant difference, if any, between relationships of males and females at the 5% level [Snedecor, Cochran, 1989]. The data on length and weight were log transformed in PAST 4.14 [Hammer et al., 2001], and one-way ANCOVA was used to calculate the *p*-value.

The length at first capture (L_c) at which 50% of fish is vulnerable for the given fishing gear was defined by calculating cumulative percentage of fish in 1-cm size classes and applying logistic function [King, 2007]:

$$P = 1/(1 + e^{-a(L-L_c)}) \,, \tag{3}$$

where P is the proportion of fish in 1-cm length classes;
L is the mid-class length;
L_c is the length at first capture;
a is the constant.

The non-linear least-squares fitting with MS Office Excel Solver was used to obtain the best fit of two parameters, L_c and a.

The same method was applied to calculate the length at first maturity (L_m). Females with ovaries and males with testis in stages 3, 4, and 5 were considered sexually mature. The cumulative percentage occurrence of mature fish of both sexes in 1-cm size groups for the studied years was determined; the logistic function (formula 3) and the non-linear least-squares fitting with MS Office Excel Solver were used to obtain L_m.

The sex ratio was determined as a number of males to number of females (M : F). The monthly sex ratios were tested for significant deviations from the expected ratio with Pearson's chi-square (χ^2) goodness-of-fit test [Snedecor, Cochran, 1989] using the formula:

$$\chi^2 = \sum (O - E)^2/E \,, \tag{4}$$

where O is observed numbers;
E is expected numbers.

The *p*-value was calculated applying CHISQ.TEST function in MS Office Excel.

To determine the spawning season, percentage occurrence of different maturity stages of gonads during various months was calculated and plotted separately for males and females together with the gonadosomatic index (hereinafter GSI). Stages 1 and 2 were considered immature and inactive; stage 3, developing/ripening; stage 4, ripe; and stage 5, running/spawning. GSI was established using the formula of R. Wydoski and E. Cooper [1966]:

$$GSI = GW/W \times 100 \,, \tag{5}$$

where GW is the gonad weight (g);
W is the total weight (g).

No clear annual growth rings were found in *S. longiceps* scales and otoliths, or they were highly inconsistent [Abdussamad et al., 2023; Al-Barwani, Prabhakar, 1989; Zaki et al., 2011]; hence, calculated length-based method was applied for age and growth estimations in the present study. To determine growth parameters in von Bertalanffy growth function (hereinafter VBGF), the Electronic Length Frequency Analysis (ELEFAN) with nonseasonal growth was used; this technique is incorporated in Tropical Fisheries Analysis (TropFishR) package [Mildenberger et al., 2017].

The age at first maturity at which fish of a given population mature for the first time was calculated from the length at first maturity using the inverse of VBGF [Mackay, Moreau, 1990]:

$$T_m = t_o - ln(1 - L_m/L_\infty)/K \,, \tag{6}$$

where T_m is age at first maturity;
t_o is the age in VBGF;
L_∞ is the asymptotic length;
L_m is the length at first maturity;
K is the growth coefficient.

The potential life span (longevity) was determined by the formula of C. Taylor [1958] which is based on the estimated parameters of VBGF:

$$T_{max} = t_o + 3/K \ , \tag{7}$$

where t_o is the hypothetical age;

K is instantaneous growth coefficient in VBGF.

The optimal fishing length (L_{opt}), the length at which the unfished cohort provides the maximum possible yield, was estimated from the equation given by R. Beverton [1992]:

$$L_{opt} = L_{\infty}(3/(3 + M/K)) \ , \tag{8}$$

where L_{∞} and *K* are parameters of VBGF;

M is the natural mortality.

The annual instantaneous rate of natural mortality (M) was estimated in TropFishR by the empirical equation of A. Then *et al.* [2015]:

$$M = 4.118K^{0.73}L_{\infty}^{-0.33} \ , \tag{9}$$

where L_{∞} (cm) is the von Bertalanffy coefficient.

The length converted catch curve method incorporated in TropFishR was employed for the calculation of total mortality coefficient (Z).

The fishing mortality (F) was determined as follows: $F = Z - M$.

The exploitation rate (E), or the fraction of deaths caused by fishing [Gulland, 1971; Ricker, 1975; Sparre, Venema, 1998], was computed as:

$$E = F/Z \ . \tag{10}$$

The exploitation ratio (U), as a fraction of the fish caught during the year, was obtained from the equation given by W. Ricker [1975]:

$$U = F/Z(1 - e^{-Z}) \ . \tag{11}$$

The annual landing (in tons) in the present study was considered as the yield (Y).

The total stock (P) in weight was estimated from the ratio [Amin et al., 2002]:

$$P = Y/U \ , \tag{12}$$

where Y is the annual average yield of the species (t);

U is the exploitation ratio.

The term standing stock biomass (B) refers to the concentration of fish populations in a given area at a given time. This can be estimated in terms of numbers or weight. In the present study, the standing stock was determined by weight using the formula [Amin et al., 2002]:

$$B = Y/F \ , \tag{13}$$

where Y is the annual yield (t);

F is the fishing mortality.

The maximum sustainable yield (hereinafter MSY) was calculated by the equation suggested by E. Cadima [Sparre, Venema, 1998; Troadec, 1977]:

$$MSY = 0.5(Y + M \times B) \ , \tag{14}$$

where Y is the total landing in a year;

M is the natural mortality;

B is the standing stock biomass in that same year.

Statistical analysis was performed using MS Office Excel and PAST 4.14 [Hammer et al., 2001].

RESULTS

Size composition. The total length of the Indian oil sardine in the studied samples in 1997 ranged between 10.0 and 21.3 cm [mean was (16.26 ± 2.04) cm], and weight ranged between 8.2 and 91.0 g [mean was (38.66 ± 14.91) g]. Females were slightly smaller than males; the mean length of females was (16.06 ± 2.14) cm, and that of males was (16.59 ± 1.81) cm. Student's *t*-test and Kolmogorov–Smirnov two-sample test showed significant differences between means and length frequency distributions of females and males ($p < 0.001$).

In the samples of 2020–2021, the total length of *S. longiceps* varied between 9.7 and 20.9 cm [mean was (16.26 ± 2.20) cm], and weight varied between 7.3 and 77.6 g [mean was (39.71 ± 14.88) g]. In contrast to the case of 1997, females were slightly larger than males; their mean length was (16.45 ± 2.30) cm, and that of males was (16.05 ± 2.03) cm. Differences between total length means and length distributions of males and females were non-significant in this case.

Comparisons between 1997 and 2020–2021 showed no significant differences in the mean length and length frequency distribution of *S. longiceps* (*t*-test, $p = 0.978$; Kolmogorov–Smirnov test, $p = 0.09$). Fish less than 14 cm contributed to about 5–6% of the catch in 1997 and 2021–2022, while the largest specimens, more than 20 cm, 10–11%. The length frequency distribution indicates three distinct modes in both cases: 13.5–14.0, 16.5–17.0, and 19.5–20.0 cm for 1997 and 14.5–15, 17.0–17.5, and 19.5–20.0 cm for 2020–2021 (Fig. 2).

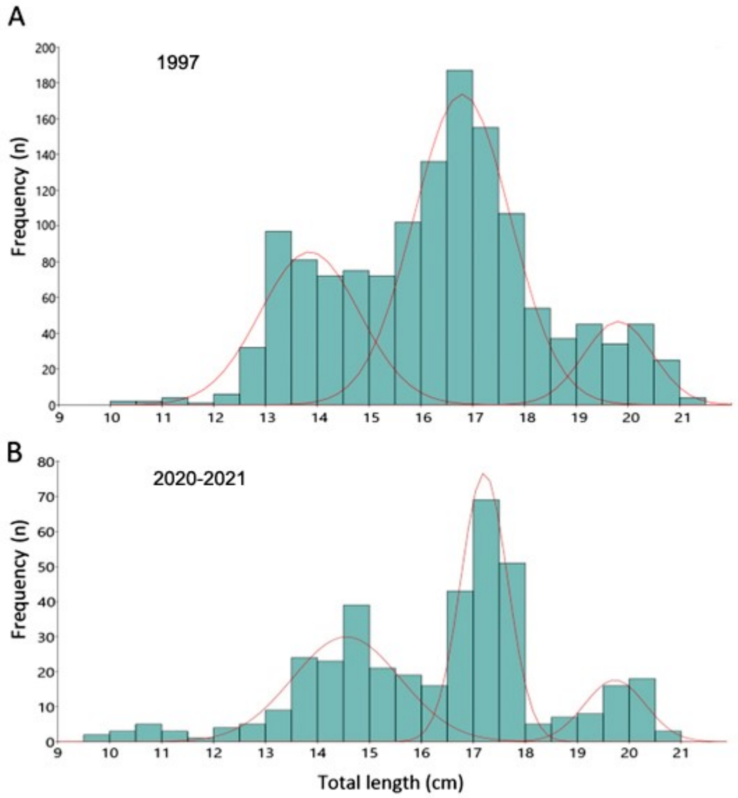

Fig. 2. Length frequency distribution of *Sardinella longiceps* from commercial catches in the Muscat region in 1997 (A) and 2020–2021 (B)

Monthly fluctuations of the mean length were very similar during 1997 and in 2020–2021 combined by months in one year (Fig. 3). Larger specimens were observed in winter time (December to February), while smaller sardines occurred mostly during summer and autumn (June to October).

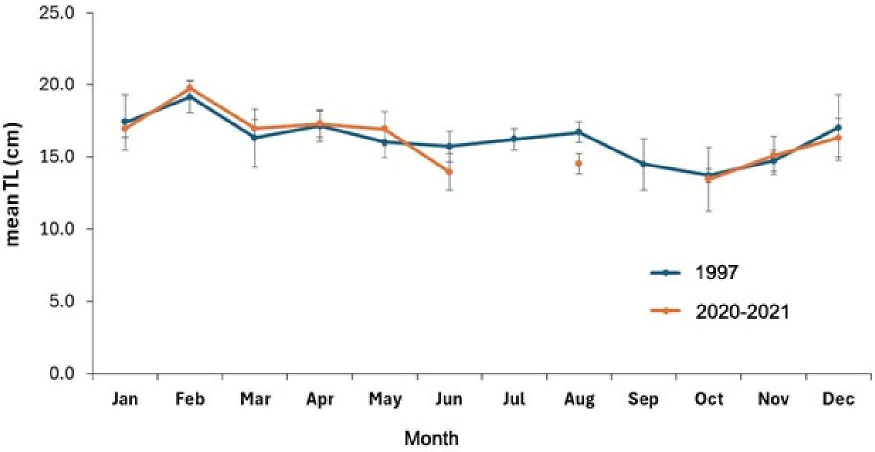

Fig. 3. Monthly fluctuations of the mean total length (TL) of *Sardinella longiceps* from the Muscat region in 1997 and 2020–2021

Length–weight relationship. Parameters a and b in the relationship between somatic weight and total length of *S. longiceps* for both sexes combined in 1997 and 2020–2022 (formula 2) were very similar (Table 1). The value of parameter b was estimated in 3.01 and 3.05, respectively, indicating a close to isometric growth in weight for the species. The coefficient of determination (r^2) was very high in both cases ranging 0.96–0.97. ANCOVA test showed no significant difference between the slopes of the length–weight relationship in 1997 and 2020–2021 ($p > 0.05$).

Table 1. Length–weight relationship of *Sardinella longiceps* from the Muscat region in 1997 and 2020–2021 (*CL*, confidence limits)

Years	*n*	a	95% *CL* a	b	95% *CL* b	r^2
1997	1,375	0.0083	0.0077–0.0089	3.0114	2.9871–3.0368	0.970
2020–2021	394	0.0076	0.0064–0.0090	3.0494	3.9867–3.1127	0.955

Length at first capture. The mean length at which 50% of fish were caught (L_c) (formula 3) was estimated to be 16.20 cm for 1997 and 16.28 cm for 2020–2021 (Fig. 4).

Length and age at first maturity. During 1997, the smallest male with ripening testis (stage 3) was 13.2 cm, and the smallest female with ripening ovary (stage 3) was 13.5 cm, while in 2020–2021, the sizes were 13.5 and 13.6 cm, respectively. Maturing testis (stage 3 and above) and maturing ovaries (stage 3 and above) were used for determination of the length at first sexual maturity. The logistic function (formula 3) showed that the mean size at the first maturity (L_m) during 1997 was 17.06 cm in males and 17.36 cm in females; during 2020–2021, it was 16.59 and 17.21 cm, respectively (Fig. 5). The result indicates that males of the Indian oil sardine mature at a slightly earlier length than females.

The age at first maturity (formula 5) was calculated for females at 1.35 years in 1997 and 1.38 years in 2020–2021.

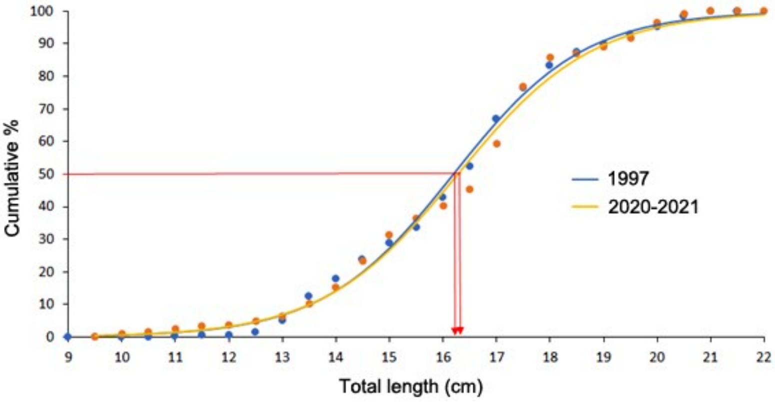

Fig. 4. Curves of cumulative percentages of catches of *Sardinella longiceps* of different sizes in the Muscat region and the length at first capture in 1997 and 2020–2021

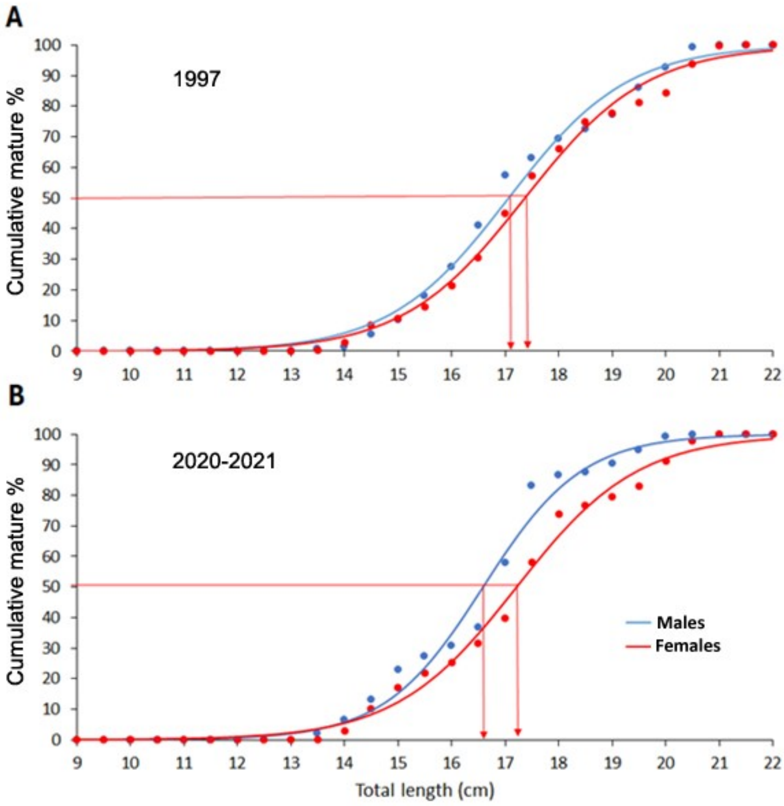

Fig. 5. Curves of cumulative percentage of mature *Sardinella longiceps* and the length at first maturity for males and females from the Muscat region in 1997 (A) and 2020–2021 (B)

Sex ratio. The sex ratio of *S. longiceps* during both studied periods was in favor of females. In 1997, females constituted 62% of the analyzed fish, and M : F = 0.60 : 1. In 2020–2021, the percentage of females was 55%, and M : F = 0.83 : 1.

The investigation of the monthly sex ratio indicated the dominance of females over males during most of the year. Males were absent in the sample from commercial catches in October 1997. The share of males was found to be larger than that of females only in June 1997, November 2021, and April 2021. The chi-square test revealed that the monthly sex ratio was significantly different from what was expected in June, August, and October 1997, while in 2020–2021, only in November. In general, the monthly sex ratio differed significantly during 1997 ($\chi^2 = 46.64$, $p = 0.002$) and non-significantly during the studied months of 2020–2021 ($\chi^2 = 12.47$, $p = 0.65$).

Spawning season. The monthly occurrence of fish with immature, ripening, and spawning gonads during 1997 indicated higher percentages of spawning males and females during November–March, in June, and during August–September. Higher GSI values were calculated for males in February and August and for females in March and August (Fig. 6).

A similar picture was observed during 2020–2021: the fish with ripening and spawning gonads dominated from November to April and in August. Higher GSI values were recorded for males during January–April and in August, and for females, during February–April and in August. Hence, spawning of the Indian oil sardine in the Muscat region may occur between November and April with a peak in March–April and again in June to September with a peak in August.

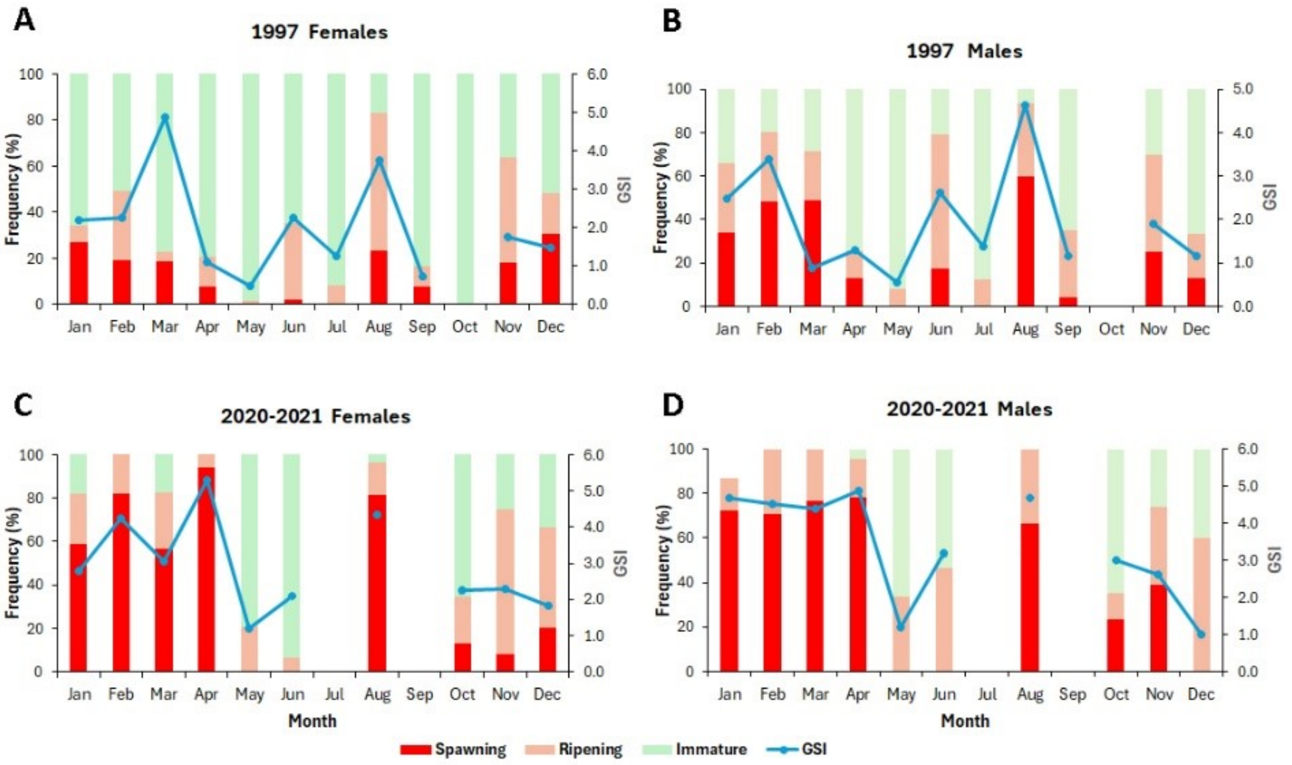

Fig. 6. Monthly changes of different gonad developmental stages (in percentage) and values of the gonadosomatic index (GSI) of *Sardinella longiceps* in the waters of Muscat: A and B, females and males, respectively, in 1997; C and D, females and males, respectively, in 2020–2021

Age, growth, and life span. Growth parameters of *S. longiceps* in VBGF estimated based on the monthly length frequency distributions using ELEFAN technique in TropFishR are provided in Fig. 7 and Table 2. In 1997 and 2020–2021, the asymptotic length (L_∞) and growth coefficient (*K*) were similar. Calculated lengths of one-, two-, and three-year-old fish were 15.7, 18.7–19.0, and 19.6–20.2 cm in 1997 and 2020–2021. Our result showed that *S. longiceps* grows very rapidly during the first year of life; then, its growth slows down, until it becomes almost negligible (after 2.5 years). From Fig. 7, new generations appeared in February 1997 and February 2021.

According to calculation by empirical formula 7, the maximum life span of the studied species was 2.36 years in 1997 and 2.60 in 2020–2021. Commercial catches of the sardine during 1997 comprised mainly one- to two-year-old fish, while in 2020–2021, fish younger by one year.

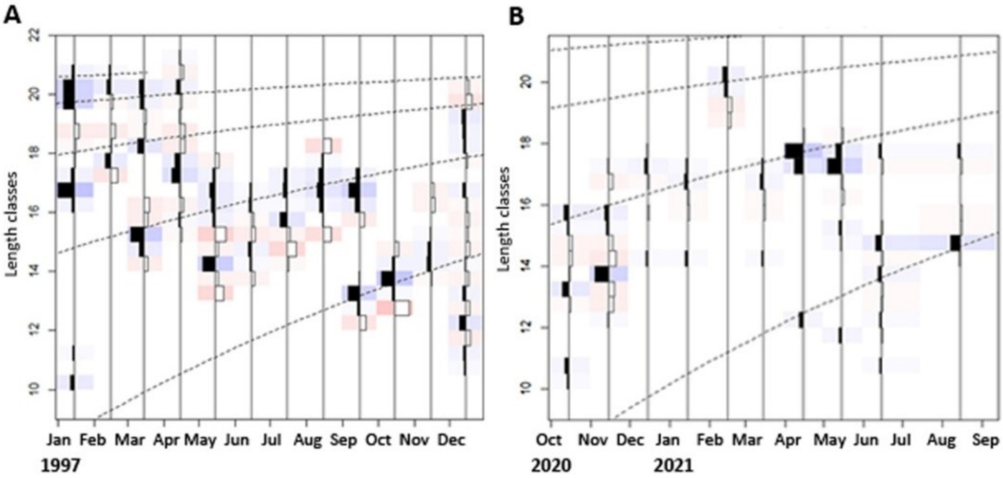

Fig. 7. Monthly length frequency distribution and growth curves for *Sardinella longiceps* from the Muscat region: A, 1997; B, 2020–2021

Table 2. Growth parameters in von Bertalanffy growth function and calculated length at different age for *Sardinella longiceps* from the Muscat region

Years	L_∞	K	t_o	Mean TL, cm					
				0.5 years	1 year	1.5 years	2 years	2.5 years	3 years
1997	20.1	1.11	–0.37	12.4	15.7	17.6	18.7	19.3	19.6
2020–2021	20.9	1.00	–0.40	12.4	15.7	17.8	19.0	19.8	20.2

Optimal fishing length. The length at which a year class (cohort) provides the maximum biomass in an unfished population (L_{opt}) was calculated (formula 8) to be 13.37 cm in 1997 and 13.90 cm in 2020–2021.

Mortality. The natural mortality (M) estimated in TropFishR package with the empirical Then's equation (formula 9) was 1.66 yr^{-1} in 1997 and 1.51 yr^{-1} in 2020–2021.

The total mortality (Z) assessed using the length converted catch curve method in TropFishR was 4.29 yr^{-1} (*SE* = 0.23) in 1997 and 4.42 yr^{-1} (*SE* = 0.19) in 2020–2021.

The fishing mortality (F) was estimated at 2.63 yr^{-1} for 1997 and 2.91 yr^{-1} for 2020–2021.

Exploitation rate, biomass, and maximum sustainable yield. *S. longiceps* fishery in the Muscat region was assessed applying several simple formulas. The exploitation rates (E) calculated based on formula 10 were 0.61 in 1997 and 0.66 in 2020–2021, and the exploitation ratios (U) determined from formula 11 were 0.60 and 0.65, respectively (Table 3). Further calculations were carried out separately for total catches of *S. longiceps* in Oman and catches in the Muscat region alone. It was assumed that in both cases, the Indian oil sardine accounted for 80% of the total sardine catches. The landings, or yield (Y), of *S. longiceps* in the Muscat region in 1997 and 2021 were very similar comprising approximately 4.3 thousand tons, while the total oil sardine landings in Oman differed by more than 26 times: from about 13.5 thousand tons in 1997 to 352 thousand tons in 2020–2021. Annual landings in Oman and the Muscat region in 1997 were about 123% of calculated MSY, and in 2021, approximately 132% of MSY. So, the effort for *S. longiceps* fishery in these years was higher than MSY indicating overfishing of the stock.

Table 3. Assessment of stock parameters of *Sardinella longiceps* based on annual landings in the Muscat region and total landings in the waters of Oman in 1997 and 2021 (t, tons)

Year	Region	E	U	Y, t	P, t	B, t	MSY, t
1997	Oman	0.61	0.60	13,412	22,353	5,100	10,939
	Muscat			4,356	7,260	1,656	3,552
2021	Oman	0.66	0.65	352,125	541,731	121,005	267,421
	Muscat			4,324	6,652	1,486	3,284

DISCUSSION

The Indian oil sardine is a small pelagic fish playing a key role in the coastal ecosystem and fisheries of Oman. The sardine landings in Oman have increased almost 27 times in the compared years: from 16,765 t in 1997 to 440,156 t in 2021. However, in the Muscat region, the sardine landings remained relatively stable: 5,445 and 5,405 t, respectively. This sharp gain in catches raises questions about possible overfishing and its effect on the population structure and the sardine stock. It also causes concerns about the future of fishing in Oman and the potential effects on other species in the ecosystem. Therefore, the population parameters of *S. longiceps* in 1997 were compared with those in 2020–2021, as well as with the results of other studies conducted in other years and areas of Oman.

According to our data, the maximum total length of *S. longiceps* was 21.3 cm in 1997 and 20.9 cm in 2020–2021. The mean length of the fish in the compared years was exactly the same (16.26 cm), and the average weight did not differ significantly: 38.66 *vs.* 39.71 g (Table 4). According to literature data, the maximum total length of *S. longiceps* in the Omani waters has reached 23.0 cm, and the maximum weight, 152.0 g, was recorded in Mahut in 2007–2009 [Zaki et al., 2021]. The mean length of this species in commercial catches in various regions of Oman in 2007–2009 ranged 16.05 to 18.42 cm, and the average weight ranged 37.96 to 57.47 g [Zaki et al., 2011].

The length–weight relationship of *S. longiceps* was similar in 1997 and 2021–2021 ($a = 0.008$; $b = 3.01\ldots3.05$) that evidences for isometric growth of the species. However, as we know, the body shape and the coefficients a and b depend on many factors, in particular, the fat content and gonad condition, and can vary significantly between seasons and between different years. S. Dutta *et al.* [2021] found that the parameter b for *S. longiceps* from the Muscat region was < 3 in some years suggesting negative allometric growth, but in other years, it was > 3 indicating positive allometric growth for this species.

We calculated the length at first capture of *S. longiceps* from the Muscat region in 1997 to be 16.20 cm, and in 2020–2021, 16.28 cm. It is quite similar and comparable to the results of S. Zaki *et al.* [2011; 2013b] but slightly smaller than the length calculated for Mahout region by N. Jayabalan *et al.* [2014].

The length at first maturity (L_m) for *S. longiceps* males and females ranged 16.6 to 17.4 cm. It has also been found that the fish attain the first maturity at the end or just after the first year of life. Most other studies have also shown that the Indian oil sardine from the Omani coast reaches maturity at about 16–18 cm and at the age of about 1 year [Al Jufaili, 2011; Siddeek et al., 1994; Zaki et al., 2011, 2012]. However, as reported in some papers, this species can mature at a smaller length (12.5–13.5 cm) [Dorr III, 1990] or larger one (18–19 cm) [Al-Anbouri et al., 2013; Zaki et al., 2021]. The age of maturation or rate of sexual maturity of a particular fish species depends on some external factors, and the most important of them are food, temperature, photoperiod, and water currents [Bhukaswan, 1980]. Notably, in most studies, when assessing the size at the first maturity of *S. longiceps* in Oman, it was found that males reach maturity at a slightly smaller length than females.

Table 4. Comparison of data on sizes, parameters of length–weight relationship (LWR), length at first capture (L_c), length at first maturity (L_m), and spawning seasons for *Sardinella longiceps* in different regions of Oman (M, male; F, female)

Years	Region	Mean TL, cm	Maximum TL, cm	Mean W, g	Maximum W, g	LWR		L_c, cm	L_m, cm	Spawning season, months	Reference
						a	b				
–	Muscat	–	–	–	–	–	–	–	12.5–13.5	Sep–Feb, Mar–Apr	Dorr III, 1990
–	Muscat	–	–	–	–	–	–	–	15.9	Apr, Oct	Siddeek et al., 1994
1997–1998	Muscat	16.47 M, 16.60 F	21.9	–	–	0.0081	3.0	–	16.7 M, 16.9 F	Feb, Mar, Aug	Al Jufaili, 2011
2005	Muscat	–	–	–	–	–	–	–	–	Mar–Apr, Aug	Al Jufaili et al., 2006
1997	Muscat	16.19	21.3	38.24	91.00	0.0063	3.0	–	–	–	Dutta et al., 2021
2004	Muscat	16.71	22.0	44.50	94.60	0.0043	3.18	–	–	–	
2005	Muscat	16.05	18.2	37.96	58.40	0.0097	2.81	–	–	–	
2006	Muscat	18.42	21.1	57.47	89.70	0.011	2.76	–	–	–	
2007	Muscat	16.34	22.0	39.58	83.60	0.0087	2.85	–	–	–	
2009	Muscat	17.76	22.0	52.34	108.00	0.0036	3.25	–	–	–	
2008–2009	Muscat	–	20.0	–	–	–	–	–	18.2	Dec–Mar, Jun–Sep	Al-Anbouri et al., 2013
2007–2009	Muscat	–	22.0	–	–	0.005	3.09	16.9	16.2–17.4 M, 16.4–17.6 F	Jan–Apr, Jun–Sep	Zaki et al., 2011
2007–2009	Mahout	–	22.8	–	–	0.001	2.91	19.3	–	–	Jayabalan et al., 2014
2007–2009	Mahout	–	23.0	–	152.0	–	–	–	18.7 M, 19.1 F	Jan–Feb, Jul–Sep	Zaki et al., 2021
2007–2009	Salalah	–	21.0	–	–	0.007	3.03	18.5	–	–	Zaki et al., 2013a
2007–2009	Sohar	–	–	–	–	–	–	–	15.6 M, 16.3 F	Feb–Mar, Sep–Oct	Zaki et al., 2012
2007–2009	Sohar	–	21.0	–	–	0.004	2.70	16.8	17.8–18.2 M, 18.2–18.4 F	Mar–Jul	Zaki et al., 2013b
1997	Muscat	16.26	21.3	38.66	91.0	0.0083	3.01	16.2	17.1 M, 17.4 F	Mar–Apr, Jun–Sep	present study
2020–2021	Muscat	16.26	20.9	39.71	77.6	0.0076	3.05	16.3	16.6 M, 17.2 F	Feb–Apr, Aug	present study

Our analysis of monthly fluctuations in occurrence of various gonad stages of males and females showed that there were ripening and spawning sardines in almost all the studied months, except for May and October 1997. This indicates that the Indian oil sardine spawns, as a rule, all year round; however, the spawning activity varies greatly throughout the year. The higher percentage of ripe and spawning fish (stages 4 and 5) was observed in January–April, August, and November–December both during 1997 and in 2020–2021. Higher GSI values were obtained in February–March and August 1997, as well as in April and August 2021. Thus, two peaks of spawning activity were detected: the first one, in February–April, and the second one, in August. This result is consistent with other investigations that also reported two spawning seasons of *S. longiceps* in the Omani waters (see Table 4). In particular, in the Muscat region, the first spawning season was observed December to April, and the second, June to October [Al Jufaili, 2011; Al Jufaili et al., 2006; Al-Anbouri et al., 2013; Siddeek et al., 1994; Zaki et al., 2011]. The spawning season of *S. longiceps* depends on environmental conditions in the sea and might vary from year to year and from region to region in Oman [Al Jufaili et al., 2006; Siddeek et al., 1994].

The sex ratio of *S. longiceps* was in favor of females – 0.60 : 1 (38% males and 62% females) in 1997 and 0.83 : 1 (45% males and 55% females) in 2020–2021 – demonstrating a significant deviation from the expected ratio of 1 : 1 ($p < 0.01$). This is consistent with the studies of S. Al Jufaili *et al.* [2011] and S. Zaki *et al.* [2011; 2012; 2021] which also showed the dominance of *S. longiceps* females over males in all analyzed regions – Muscat, Mahout, Salalah, and Sohar – in 1997–1998 and 2007–2009. Combining our material with literature data [Zaki et al., 2011] on abundance of males and females, we concluded that the Indian oil sardine has an overall female-biased sex ratio 0.64 : 1 (39% males and 61% females) in the Omani waters. This pattern means increasing egg production *per* population biomass for the species. The sex ratio provides basic information for assessing the reproductive potential and estimating stock size of fish populations. There is a wide variation in sex determination systems in fish, where sex can be determined by environmental factors (mainly temperature) and genetic ones [Baroiller et al., 2009; Conover, Heins, 1987]. In this case with *S. longiceps*, the sex ratio seems to be determined primarily by genetic factors.

S. longiceps age and growth are difficult to establish by studying otoliths and other hard parts (scales and vertebrae), as there are no clear annual rings [Al-Barwani, Prabhakar, 1989; Zaki et al., 2011]. However, some attempts were made in early works to analyze the age of sardines [Balan, 1964; Hornell, Naidu, 1924; Nair, 1949, 1952]. These investigations have shown that the Indian oil sardine has a rapid growth rate and a life span of about three years, and the fish reach sexual maturity at about 15 cm in length at the age of one year [Hornell, Naidu, 1924] or two years [Nair, 1952]. Recently, age and growth of *S. longiceps* from Indian waters were assessed by three approaches: interpretation of microstructures on hard parts (mainly otoliths), modal progression analysis of length frequency data of fish caught in commercial fishing, and direct measurement of sardines reared in open sea cages on natural food during 11 months [Abdussamad et al., 2023]. The authors reported a much faster growth rate (K of 1.57 and 1.76 yr^{-1}) for this species compared to values in previous investigations. However, they also found a significant difference in the sardine growth rate between different years, when, according to their results, one-year-old fish reached 20.4 cm in 2011–2013 and only 15.6 cm in 2014–2017.

Studies on *S. longiceps* age and growth in the Omani waters are largely based on length frequency analysis [Al-Anbouri et al., 2011; Dutta et al., 2024; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b, 2021] which was also used in the present research. Overall, our data showed similar growth parameters for the sardine in 1997 and 2020–2021. When comparing our results with those of other investigations, it can be noted that we obtained lower L_∞ values, except for values in the work of M. Siddeek *et al.* [1994], but *K* values are similar to those in most previous works (Table 5). Some differences in growth parameters with the results of other authors may be related to calculation procedures, as we used ELEFAN from TropFishR package, while S. Zaki *et al.* [2011; 2013a; 2013b; 2021] and N. Jayabalan *et al.* [2014] applied ELEFAN routine incorporated in LFDA5 of Fish Stock Assessment Software (FMSP) developed by MRAG Ltd [Kirkwood et al., 2003], and S. Dutta *et al.* [2024] calculated L_∞ and *K* values using ELEFAN I from FiSAT II [Gayanilo et al., 2005]. However, in general, all the results on *S. longiceps* growth and life span presented in Table 5 are comparable, and the observed differences may be due to variations in growth rate in different years and regions which depend on environmental conditions and food availability, but have no clear relationship with fishing intensity.

Table 5. Summary of *Sardinella longiceps* growth parameters, mortality, and exploitation rate in the waters of Oman

Years	Region	L_∞, cm	*K*, yr^{-1}	t_o, yr	T_{max}, yr	Z, yr^{-1}	M, yr^{-1}	F, yr^{-1}	E	Reference
–	Muscat	19.72	0.986	–	3.75	–	–	–	–	Siddeek et al., 1994
2008–2009	Muscat	22.02	1.21	−0.01	2.5	4.11	2.21	1.91	0.46	Al-Anbouri et al., 2011
2007–2009	Muscat	23.18	1.21	−0.21	2.0	4.17	2.22	1.99	0.47	Zaki et al., 2011
2007–2009	Mahout	23.00	1.33	−0.09	2.5	3.66	2.21	1.45	0.40	Jayabalan et al., 2014
2007–2009	Salalah	23.02	1.57	−0.49	2.0	4.65	2.45	2.20	0.47	Zaki et al., 2013a
2007–2009	Sohar	23.00	1.40	−0.15	2.5	3.97	2.28	1.69	0.43	Zaki et al., 2013b
1997	Muscat	22.80	1.10	−0.08	2.64	4.69	1.08	3.61	0.77	Dutta et al., 2024
2004	Muscat	23.63	1.20	−0.07	2.43	4.50	1.13	3.37	0.75	
2007	Muscat	23.42	1.0	−0.09	2.91	1.89	1.01	0.88	0.47	
2009	Muscat	23.42	0.94	−0.10	3.10	6.30	0.97	5.33	0.85	
1997	Muscat	20.1	1.11	−0.37	2.36	4.29	1.65	2.63	0.61	present study
2020–2021	Muscat	20.9	1.10	−0.40	2.60	4.42	1.51	2.91	0.66	present study

The Indian oil sardine has a high rate of natural mortality (M) previously estimated based on the empirical equation of D. Pauly [1980]: 2.21 to 2.45 yr^{-1} [Al-Anbouri et al., 2011; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b, 2021]. However, according to S. Dutta *et al.* [2024], it ranged between 0.97 and 1.13 yr^{-1} (see Table 5). In fact, natural mortality is very difficult to determine, but this parameter is pretty important in most stock assessments. Many methods have been developed to predict natural mortality, and one of the most popular is Pauly's empirical formula based on growth parameters and water temperature [Pauly, 1980]. Recently A. Then *et al.* [2015] proposed new formulas for estimating natural mortality using data from 200 fish species; those are based on maximum age (t_{max}) or asymptotic length (L_∞). This method is included in TropFishR package; therefore, we used it and calculated *S. longiceps* natural mortality at 1.65 yr^{-1} for 1997 and 1.51 yr^{-1} for 2020–2021. In the case of applying Pauly's formula, the coefficient M was estimated at 2.15 and 2.11 yr^{-1}, respectively.

Our estimates of the total mortality (Z) were similar to those for the years studied and to results of most other authors [Al-Anbouri et al., 2011; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b, 2021]. It can be noted that Z estimates of S. Dutta *et al.* [2024] varied greatly, and for 2007 and 2009, they differed significantly from other results. With the chosen approach, values of natural and total mortalities determine further calculations of fish population parameters, such as fishing mortality, exploitation rate, and, together with catch data, also total stock, standing stock, and MSY. So, the exploitation rate (E) was > 0.5 in the case of using estimates of M according to Then's formula and close to 0.5 if we applied the Pauly's formula.

Previous studies have shown that *S. longiceps* landings in different regions of Oman in some years within 1997–2009 were either lower or close to the optimal level [Al-Anbouri et al., 2011; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b]. On the other hand, S. Dutta *et al.* [2024] reported that the stock of the species was largely overexploited in this time. From our results, *S. longiceps* stock was overexploited in 1997, as well as in 2020–2021. J. Gulland [1983] recommends 0.5 as a suitable exploitation rate for fish stocks in temperate water. However, fish forming stocks in tropical and subtropical areas are characterized by short life cycles and rapid growth, and they can sustain high exploitation rates [Wang et al., 2012].

Conclusion. Our results on biological and population parameters of *Sardinella longiceps* for 1997 and 2020–2021, as well as their comparison with results of similar investigations in other years, indicate that its life-history and population parameters have not changed significantly because of a sharp increase in the sardine fishing along the Omani coast in recent years. The present study is based on data from the Muscat region of the Sea of Oman, where sardine catches were almost identical in compared years, while a sharp rise in the sardine catches occurred in the southern regions of the country, Al Wusta and Al Sharqiyah, located in the Arabian Sea. Many investigations have shown that population parameters of *S. longiceps* vary noticeably in different areas and in different years. It is necessary to analyze the structure of stocks of the Indian oil sardine along the Omani coast applying modern genetic techniques.

It would be more appropriate to use otoliths for determining *S. longiceps* age. Data generated from otolith study would aid in better eco-biological understanding of the species, in establishing precise time of birth, and in identifying cohorts that support the fishery and possible interregional migration of this fish. The sardine stock biomass and landings have been highly variable in the long-time series. The present approximate estimations based on growth, mortality, and landing data do not provide true dynamics of the sardine stock; so, it is necessary to apply integrated analytical models that include catch-at-age data, catch-*per*-unit effort, and stock-recruitment model together with direct assessment methods, such as acoustic, trawling, and aerial survey, as well as egg and larvae surveys. The use of direct and indirect methods can help to improve the accuracy and reliability of the sardine stock assessments, and it is essential for the fishery management and development of the fishery sector.

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СРАВНЕНИЕ ПОПУЛЯЦИОННЫХ ПАРАМЕТРОВ ЖИРНОЙ ИНДИЙСКОЙ САРДИНЫ *SARDINELLA LONGICEPS* ИЗ РАЙОНА МАСКАТА (СУЛТАНАТ ОМАН) В 1997 И 2020–2021 ГГ.

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Жирная индийская сардина *Sardinella longiceps* играет ключевую роль в прибрежной экосистеме и в рыболовстве Омана. Общий объём вылова сардин вдоль побережья Омана резко возрос — примерно с 17 000 т в 1997 г. до 440 000 т в 2021 г. Сравнение размерной структуры, соотношения длины и массы тела, динамики зрелости, периодов нереста, показателей роста, смертности и некоторых популяционных характеристик *S. longiceps* из района Маската в 1997 и 2020–2021 гг., а также сопоставление данных, полученных в ходе более ранних исследований в Омане, демонстрирует, что биологическая структура популяции в исследуемые годы была относительно стабильной. Уровень эксплуатации запаса в то время превышал 0,5, то есть запас *S. longiceps* в водах Омана подвергался чрезмерной эксплуатации (при этом известно, что сардина способна выдерживать высокие уровни). Биологические данные, полученные в ходе настоящей работы, могут служить основой для управления промыслом этого вида, однако необходимо продолжать мониторинг уловов, чтобы собирать и анализировать более длительные временны́е ряды биологической информации.

Ключевые слова: жирная индийская сардина, *Sardinella longiceps*, размерный состав, репродуктивные характеристики, рост, смертность, запас, многолетняя изменчивость, Маскат, Оманский залив

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CRITICAL INTENSITY OF SWIRLING FLOWS OF A SUSPENSION AND PRODUCTIVITY IN BATCH CULTURE OF *ARTHROSPIRA (SPIRULINA) PLATENSIS* UNDER DIFFERENT LIGHT CONDITIONS

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The paper provides results of the experimental study of batch cultures of *Arthrospira (Spirulina) platensis* under conditions of critical intensity of swirling flows at different size of the working layer (the optical path). As shown, despite a 10-fold increase in the intensity of vortex mixing, the productivity of the culture decreased by 2 times, when the working layer rose by 3 times. Notably, for photosynthetic microorganisms, the key factor determining the productivity in the culture is the spatial irradiation inside cell suspension (the working layer) but with the intensity of suspension stirring taken into account. The conditions of cultivation of photosynthetic cells under which the working layer differs by 2 times, but the productivity in the culture remains the same, are experimentally demonstrated.

Keywords: vortex mixing, spirulina, photobioreactor

The productivity of photosynthetic microorganism cultures is mediated by many factors. However, when designing industrial photobioreactors (hereinafter PBRs), the key parameters are the optical path (working layer) and the intensity of cell suspension mixing. Importantly, these two parameters affect much the productivity of the cultivation system and also determine the PBR design features and its operating modes. As proven experimentally, in industrial microbiology, one of the most promising methods of the cell suspension mixing is the generation of its tornado-like vortex motion, *i. e.*, the creation of closed swirling quasi-stationary flows inside the PBR working volume [Gevorgiz et al., 2021; Mertvetsov и др., 2002; Naumov et al., 2023a; Patent 1779690 A1 SU, 1992; Patent 2099413 C1, 1992; Patent EP 1120460 B1, 1998; Patent EP 27446382 A1, 2011]. The vortex method allows for effective mixing of the culture simultaneously providing three-dimensional circulation and meridional motion of the medium. At the same time, it is gentle enough: with no water hammer, turbulence, cavitation, increased shear stresses, and mechanical effect on cells. The mixing efficiency of the vortex formed in the suspension is the highest when radiuses of the vortex PBR and the working layer are equal [Naumov et al., 2023b]. Under such conditions, complete meridional circulation of the medium is ensured throughout the working volume, while losses due to viscous friction against stationary walls of the reactor are small. However, unlike heterotrophic microorganisms, phototrophs must be provided with light energy in all layers of the working volume; therefore, industrial PBRs are always designed with a thin working layer [Shtol' et al., 1976]. Despite numerous publications focused on studying the effect of radiance and mixing intensity on the productivity of photosynthetic cells [Bitog et al., 2014; Wang, You, 2013; Ye et al., 2018a, b; Xu et al., 2020], there is still the question of increasing the yield in optically dense cultures by a boost in the swirling intensity and, consequently, the speed of the swirling flow.

The aim of this work is to study batch cultures of lower phototrophs under conditions of critical intensity of swirling flows at different sizes of the working layer (optical thickness of the culture).

MATERIAL AND METHODS

The research was carried out at the laboratory of advanced energy-efficient technologies at the Novosibirsk State University (Novosibirsk). The work investigated a unialgal culture of a cyanobacterium *Arthrospira (Spirulina) platensis* (Nordstedt) Gomont (strain IBSS-31) from the collection of microalgae and cyanobacteria cultures of the IBSS core facility "Collection of Hydrobionts of the World Ocean" (Sevastopol). For intensive cultivation of the cyanobacterium, the Zarrouk's medium [1966] was used, with the composition as follows ($g \cdot L^{-1}$): $NaHCO_3$, 16.8; $NaNO_3$, 2.5; $KH_2PO_4 \times 2H_2O$, 0.66; K_2SO_4, 1.0; NaCl, 1.0; Na_2EDTA, 0.08; $FeSO_4 \times 7H_2O$, 0.01; $CaCl_2$, 0.04; $MgSO_4 \times 7H_2O$, 0.2; H_3BO_3, 2.86×10^{-3}; $MnCl_2 \times 4H_2O$, 1.81×10^{-3}; $ZnSO_4 \times 7H_2O$, 0.222×10^{-3}; $CuSO_4 \times 5H_2O$, 0.079×10^{-3}; MoO_3, 0.015×10^{-3}; NH_4VO_3, 0.02296×10^{-3}; $Co(NO_3)_2 \times 6H_2O$, 0.04398×10^{-3}; $K_2Cr_2(SO_4)_4 \times 24H_2O$, 0.0960×10^{-3}; $NiSO_4 \times 7H_2O$, 0.04785×10^{-3}; $Na_2WO_4 \times 2H_2O$, 0.01794×10^{-3}; and $Ti_2(SO_4)_3$, 0.0960×10^{-3}. This nutrient medium was prepared using distilled water. To maintain a constant pH level (8.4), CO_2 was added to the culture with a pH monitor from a cylinder.

All the tests were carried out with the culture adapted to experimental conditions in two vortex-type PBRs. PBR-1 was a cylindrical container with a submerged rotating disk of radius R_1 being 145 mm. The rotating disk generated swirling flows inside the suspension, and this allowed eliminating stagnant zones in the working volume. To generate a vortex motion in PBR-2, a swirling air flow was created above the suspension by rotating a blade wheel (an activator). As a result, the vortex formed above the suspension due to air friction on the phase interface and the pressure difference between the periphery and the center of the gas-air vortex involved the cell suspension at the interface in tangential motion and generated swirling meridional circulation throughout the working volume ascending near the axis and descending at the reactor periphery [Naumov et al., 2023b]. To stabilize the phase interface in PBR-2, a free-floating flat washer was used (Fig. 1). The radius of the flat washer R_2 was 76 mm; the radius of a hole in the washer r_2 was 16 mm. The rotation speeds of the flat washer in PBR-1 and the activator in PBR-2 were constant throughout the batch cultivation and determined the culture mixing intensity.

The experiments were carried out at a constant temperature and 24-hour illumination. White CRI90 3000K LEDs were used as a light source; those created the same irradiance, 20 $W \cdot m^{-2}$, on the PBR working surface in all the tests. The irradiance was calculated based on data of a Yu-116 luxmeter, the relative visibility spectrum, and spectral characteristics of the LEDs provided by the manufacturer [Gevorgiz, Malakhov, 2018]. In the experiment No. 1, in PBR-1, the working layer h_1 was 150 mm (suspension volume V_1 was 39.6 L), and the disk rotation frequency was 3.4 Hz ($\omega_1 = 204$ rpm). The maximum (critical) speed of the suspension motion in swirling flows was selected in such a way that the interface did not oscillate or deform, *i. e.*, the working layer in all directions remained the same. Under conditions of the experiment No. 1, the value of the tangential velocity of motion ν_1 was 3.10 m·s^{-1}. Conditions of the experiment No. 2 were similar to those of the experiment No. 1, but the working layer was reduced 3 times, to h_2 = 50 mm (V_2 = 13.2 L), and the disk rotation frequency was reduced 10 times, to 0.34 Hz (ω_2 = 20.4 rpm), with the tangential velocity ν_2 being 0.31 m·s^{-1}. In the experiment No. 3, in PBR-2, the working layer h_3 was 105 mm (V_3 = 2.7 L), the activator rotation frequency was 1,200 rpm, and the flat washer rotation frequency was 0.88 Hz (ω_3 = 52.8 rpm). The maximum tangential velocity of motion ν_3 was 0.42 m·s^{-1}. Conditions of the experiment No. 4 were similar to those of the experiment No. 3, but the working layer h_4 was 50 mm (V_4 = 1.27 L), and the rotation frequency of the activator was reduced to 15 Hz (900 rpm); accordingly, the rotation frequency of the flat washer decreased to 0.7 Hz (ω_4 = 42 rpm). The maximum value of the tangential velocity ν_4 was 0.33 m·s^{-1}.

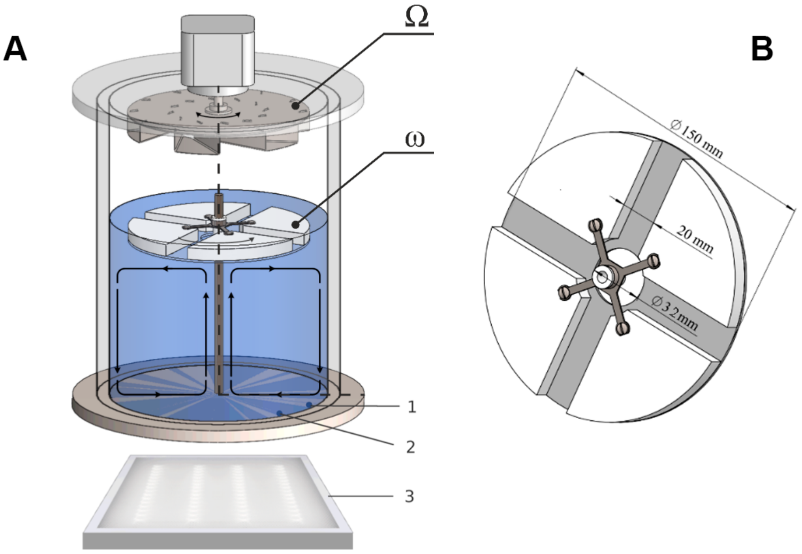

Fig. 1. Schematic diagram of gas-vortex bioreactor (A); flat washer (B). In the diagram: 1, pH sensor position; 2, point of CO_2 injection into the suspension; 3, radiation source

Throughout the experiments, the culture biomass was assessed daily by measuring the attenuation of the light flux at a wavelength of 750 nm by a layer of the cell suspension using a KFK-2 concentration photometer (T_{750}, %; a 5-mm cuvette) with a subsequent transition to optical density $D_{750} = -\lg (T_{750} / 100)$ and to biomass $B = D_{750} \times 0.85$ (g d. m.·L^{-1}) [Gevorgiz et al., 2005]. The standard deviation of the culture density measurements in all the experiments did not exceed 0.02 g d. m.·L^{-1}. The maximum productivity in the culture was calculated for a linear section of the cumulative curve applying the following expression:

$$B(t) = P_m \times (t - t_L) + B_L \ ,$$

where B is the biomass, g d. m.·L^{-1};

P_m is the maximum productivity, g d. m.·L^{-1}·day^{-1};
t is time, days;
t_L is the initial moment of the linear section of the cumulative curve, days;
B_L is biomass at the moment t_L.

RESULTS AND DISCUSSION

In optically dense cultures, because of dark respiration and costs of maintaining the structure, a drop in productivity is always observed [Avsiyan, Lelekov, 2020; Torzillo et al., 1991]. Due to the two-stage nature of the photosynthesis process, it can be assumed as follows: an increase in the mixing intensity will reduce the time cells spend in layers with irradiance below the photosynthesis compensation point which will govern a rise in productivity. This will allow increasing the yield in industrial PBRs with a thick working layer.

Many experimental studies have shown that light conditions of cultivation are the key factor mediating the productivity in a culture [Avsiyan, Lelekov, 2020; Lelekov et al., 2020; Trenkenshu et al., 1981]. Interestingly, not only the surface irradiance is important, but also the distribution of radiation energy within the cell suspension [Novikova, 2017; Qiang et al., 1998] which much depends on the current culture density [Richmond, 2000]. For light-limited cultures, the productivity value tends to depend on irradiance linearly; thus, for *A. platensis*, linearity is observed at 5–30 $W \cdot m^{-2}$ [Lelekov et al., 2020]. However, for intensively mixed cultures, this pattern is not always observed. For example, the results of our experiments (Figs 2, 3) show that the intensity of mixing does boost the productivity of cultures, but not linearly. Therefore, studying the effect of light conditions on productivity, it is necessary to take into account the intensity of the culture mixing as well.

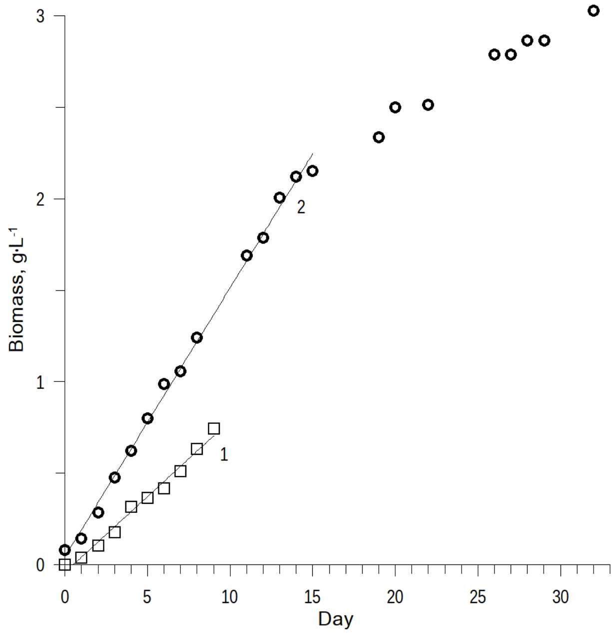

Fig. 2. Density dynamics of *Arthrospira (Spirulina) platensis* batch culture with various working layer size and vortex mixing intensity. The standard deviation of measurements does not exceed 0.02. 1, experiment No. 1: $h_1 = 150$ mm; $\omega_1 = 204$ rpm; $v_1 = 3.10\ m \cdot s^{-1}$; $B_1 = 0.08 \times t - 0.04$. 2, experiment No. 2: $h_2 = 50$ mm; $\omega_2 = 20.4$ rpm; $v_2 = 0.31\ m \cdot s^{-1}$; $B_2 = 0.15 \times t + 0.05$

The intensity of the cell suspension mixing is always limited: either by the design of the PBR or by species-specific features of cells cultured. In particular, for a plane-parallel PBR, at a certain critical intensity of air bubbling, abundant foam occurs hindering the cultivation process [Kubar et al., 2022; Shtol' et al., 1976]. For a pool-type PBR, at a certain critical speed of motion of a mechanical stirrer, due to local pressure swings and an increase in temperature, cultured cells die [Mazzuca Sobczuk et al., 2006]. Microalgae cells are destroyed by the use of pumps [Jaouen et al., 1999], filters [Vandanjon et al., 1999], and sprinklers [García Camacho et al., 2000]. Moreover, cells are also susceptible to damage by gas bubbles and high turbulence of the culture medium [Silva et al., 1987]. Therefore, in practice, for the cultivation of photosynthetic microorganisms, the suspension is mixed not intense enough, while in large-volume PBR, the key factor affecting productivity is almost always the spatial irradiance (the working layer). According to our data, despite the maximum intensity of the suspension vortex mixing ($\nu_1 = 3.097$ m·s^{-1}) in a layer h_1 of 150 mm, the productivity in the batch culture was 2 times lower (see Fig. 2) compared to that in a thinner working layer ($h_2 = 50$ mm, $3h_2 = h_1$) and low mixing intensity ($\nu_2 = 0.3097$ m·s^{-1}, $10\nu_2 = \nu_1$). Notably, with a 3-fold increase in the working layer, the productivity decreased not by 3 times, as might be expected for a light-limited culture, but by 2 times ($P_1 = 0.08$ g d. m.·L^{-1}·day^{-1}, $P_2 = 0.15$ g d. m.·L^{-1}·day^{-1}). This is due to a 10-fold rise in the intensity of the cell suspension mixing.

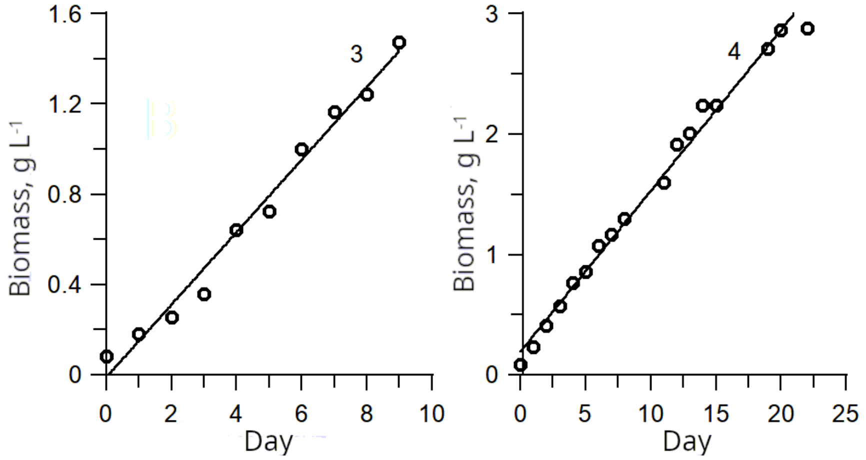

Fig. 3. Density dynamics of *Arthrospira (Spirulina) platensis* batch culture with various working layer size and vortex mixing intensity. The standard deviation of measurements does not exceed 0.02. 3, experiment No. 3: $h_3 = 105$ mm; $\omega_3 = 52.8$ rpm; $\nu_3 = 0.42$ m·s^{-1}; $B_3 = 0.08 \times t - 0.04$. 4, experiment No. 4: $h_4 = 50$ mm; $\omega_4 = 42.8$ rpm; $\nu_4 = 0.33$ m·s^{-1}; $B_4 = 0.15 \times t + 0.05$. The productivity of *A. (S.) platensis* culture (angle of inclination) is similar under different light conditions

When increasing the intensity of the culture mixing and shifting the working layer, there can be a cultivation mode established in which a 2-fold increase in the working layer will not change the culture productivity. Fig. 3 shows two cumulative curves characterized by almost the same productivity ($P_3 = 0.16$ g d. m.·L^{-1}·day^{-1}, $P_4 = 0.15$ g d. m.·L^{-1}·day^{-1}), while the working layer of the cultures differed by 2 times ($h_3 = 105$ mm, $h_4 = 50$ mm, $h_3 = 2h_4$). Accordingly, when culturing microalgae and cyanobacteria in industrial PBRs, in order to obtain the maximum yield with considering costs of mixing a unit volume of the suspension, it is necessary to set the maximum permissible intensity of the culture mixing and increase the working layer to a certain limit value the culture productivity does not drop at. This approach will definitely rise the yield, especially during the industrial cultivation of photosynthetic microorganisms under natural light conditions (in particular, in areas with low solar radiation flux) and during cultivation in autumn and winter [Chekushkin et al., 2022].

Conclusion. Along with light conditions, an important factor governing the productivity of microalgae and cyanobacteria culture is its mixing. The effect of this factor is especially evident when increasing the working volume and working layer of the cell suspension in industrial photobioreactors.

Increasing the intensity of the culture mixing up to certain critical values will allow obtaining the maximum yield at fixed irradiance. Currently, theoretical concepts of mixing of photosynthetic cells in culture are poorly developed; therefore, to control growth processes and find optimal solutions, it is necessary to build models of substrate-dependent growth under the effect of two factors: mixing and light supply of cells. This is a fairly complex interdisciplinary task requiring the introduction of new quantitative criteria that allow to compare different mixing methods in photobioreactors of various designs and to assess formally the intensity of cell suspension mixing in the working volume.

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КРИТИЧЕСКАЯ ИНТЕНСИВНОСТЬ ЗАКРУЧЕННЫХ ПОТОКОВ СУСПЕНЗИИ И ПРОДУКТИВНОСТЬ НАКОПИТЕЛЬНОЙ КУЛЬТУРЫ *ARTHROSPIRA (SPIRULINA) PLATENSIS* ПРИ РАЗЛИЧНЫХ СВЕТОВЫХ УСЛОВИЯХ

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Представлены результаты экспериментального исследования накопительных культур *Arthrospira (Spirulina) platensis* в условиях критической интенсивности закрученных потоков при различной величине рабочего слоя (оптического пути). Показано: несмотря на повышение интенсивности вихревого перемешивания в 10 раз, при увеличении рабочего слоя в 3 раза продуктивность культуры уменьшалась в 2 раза. Отмечено, что для фотосинтезирующих микроорганизмов ведущим фактором, определяющим продуктивность культуры, является пространственная облучённость внутри суспензии клеток (рабочий слой), но с учётом интенсивности перемешивания суспензии. Экспериментально продемонстрированы условия культивирования фотосинтезирующих клеток, при которых рабочий слой отличается в 2 раза, но продуктивность культуры при этом остаётся неизменной.

Keywords: vortex mixing, spirulina, photobioreactor

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THE FIRST LOCAL MOVEMENTS OF THE KITTIWAKE *RISSA TRIDACTYLA* (LINNAEUS, 1758) ABOVE THE CITY BLOCKS OF MURMANSK

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All over the world, new manifestations of synanthropic tendencies for various bird species are constantly observed. This paper provides data on *Rissa tridactyla* occurrence in Murmansk. Observations were carried out on the route of the summer daily migration of the kittiwake, formed for the first time in 2020, through the center of Murmansk, where this species has not been encountered before. Some features of the flight during the first (2020) and the second year (2021) of the route existence are determined. The approximate abundance of flying birds has been established: 1,500 ind. *per* day. The occurrence of this type of bird activity can be considered as the first stage of the kittiwake adaptation to environment of the residential part of the city.

Keywords: kittiwake, *Rissa tridactyla*, city, lake

Urban ecosystems are periodically subjected to factors mediating shifts in both species composition and demographic indicators of certain species. The number of species in cities is changing, often rising in recent years [Krasnobaev, Konstantinov, 2008; Podolsky, Lobachev, 2016]. This may partly result from the aging of urban ecosystems, as “any biocenosis tends to gradually increase in species richness” and “old biocenoses are generally richer than young ones” [Dajor, 1975]. Due to various circumstances, some species may appear in a biocenosis for the first time, while other ones, previously occurring there, may change their status. The process of species synurbization, when animals adapt to urban environments, has been ongoing for over 100 years, with certain species having their own history of gradual adaptation to urban landscapes in both geographical dimension and time [Luniak, 2004].

This report focuses on the first registration of a migration route of a seabird, the kittiwake *Rissa tridactyla* (Linnaeus, 1758), over the residential part of Murmansk. The route of the summer daily migration of birds was first recorded in 2020; it stretches from the Kola Bay (natural habitat of the kittiwake) to the freshwater Lake Bolshoye and passes through the center of Murmansk which is characterized by high intensity of traffic and pedestrian flow. This route persisted in subsequent years.

The relevance of this work lies in providing information on the first appearance of *R. tridactyla* in the residential area of Murmansk which may be the initial stage of synurbization for this species.

The aim of the study was to describe the newly formed route of *Rissa tridactyla* summer daily migration through the center of Murmansk.

MATERIAL AND METHODS

Observations of the flight were carried out along linear walking routes and from a stationary observation point (Fig. 1). A 12× binocular was used.

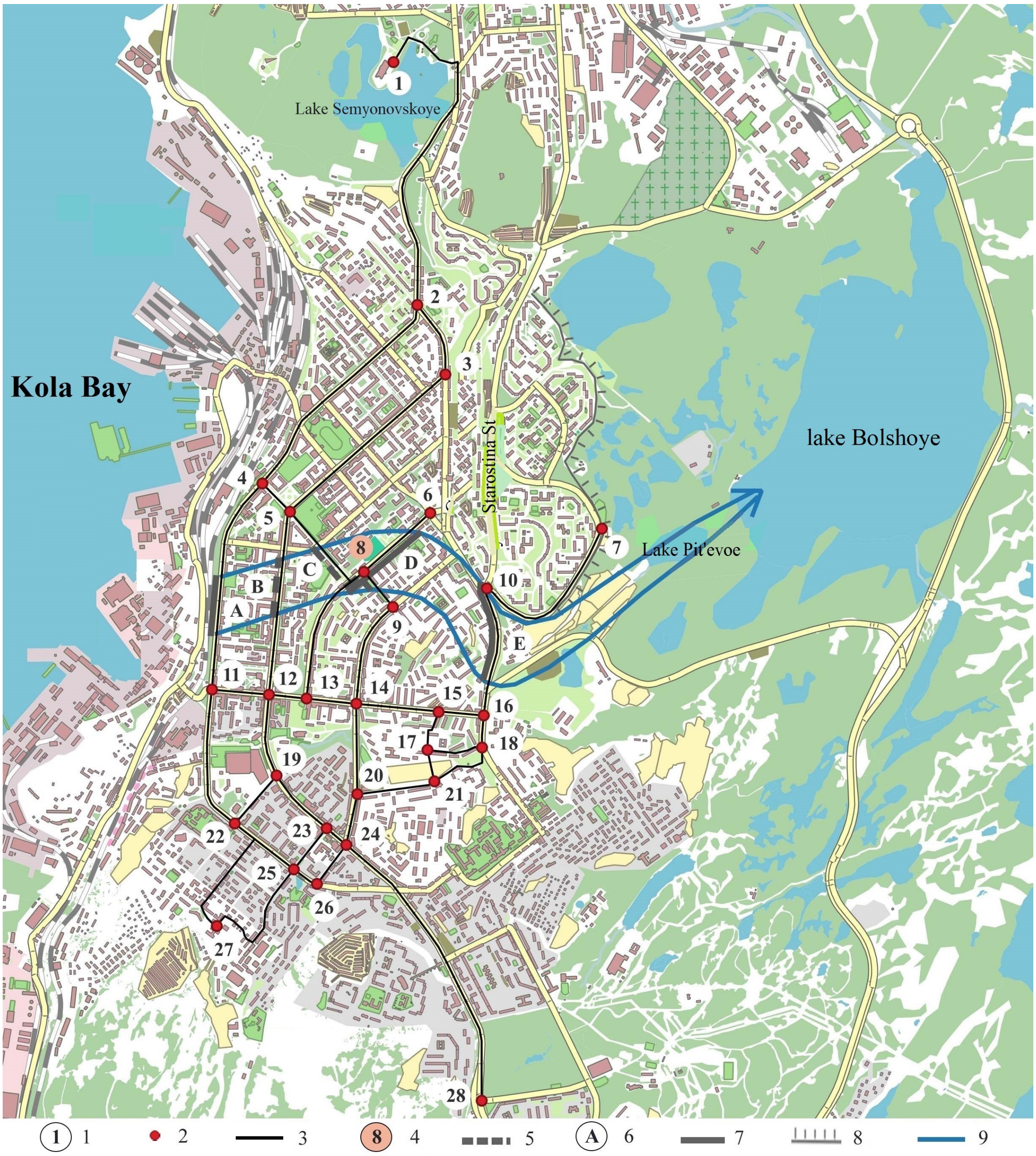

Fig. 1. Scheme of observation routes and trajectory of *Rissa tridactyla* flight over Murmansk: 1, 2, extreme points of the observation routes; 3, the observation routes; 4, stationary observation point; 5, route areas where the kittiwake was observed, with no fixing of the flyway width; 6, 7, route areas where the kittiwake was observed, with fixing of the flyway width; 8, steep cliff; 9, approximate borders of the flyway

On the routes, we recorded spots of the kittiwake movement or absence of birds. Some routes (segments between points 1–28 in Fig. 1) ranged 200–2,000 m in length. The number of surveys *per* year was 2–440. Over two years, the total length of survey routes was approximately 2,300 km. From the stationary observation point, the abundance of kittiwakes flying over the city was recorded from 16 July to 8 August, 2020, and from 14 July to 6 August, 2021. The entire flyway width was visually covered. A series of 30-minute surveys was carried out at different times of the day (between 7:00 and 21:00). The abundance of birds in flying groups, their direction, and flight altitude were registered. Flight altitude was estimated visually relative to the known height of nearby buildings. Weather conditions did not differ much: in observation days, the mean air temperature was +16 °C in 2021 and +17 °C in 2022; the mean wind speed was of 4 $m \cdot s^{-1}$ in both years. There was no precipitation.

The daily density of *R. tridactyla* flow was approximated by a normal distribution, and the total abundance of kittiwakes flying to the lake was estimated using the formula:

$$f(x) = \frac{1}{\sigma(\sqrt{2\pi})} \exp\left[\frac{-(x-a)^2}{2\sigma^2}\right] ,$$

where x is the variable (time, h);

a is the mean, or expected value, for x;

δ is the standard deviation for x.

Assuming that these two curves are sufficiently close, we determined the total abundance of birds flying to the Lake Bolshoye; MS Office Excel was used for the calculations. By adjusting the parameters a and δ, the one can approximate observation results as closely as possible to the normal distribution curve, and the value of the integral distribution function F(x) for x = ∞ can provide the total abundance N.

RESULTS

R. tridactyla migration route over Murmansk, from the Kola Bay area to the lake and back, covered the central part of the city, where traffic is the heaviest. The flyway width was about 300 m (see Fig. 1). Kittiwakes did not fly in a straight line: on the second half of their route, they skirted a hill with high-rise buildings.

The final destination of the flight is the Lake Bolshoye located 3.7 km from the bay and 0.8 km from the residential part of the city. The Eastern Bypass Road, with its constant traffic, runs near the eastern shore of the lake. During the observation period, 200–300 kittiwakes were encountered on the Lake Bolshoye surface during the day. Interestingly, kittiwakes ignored the smaller Lake Pit'evoye which lies under the flyway and is situated 0.2 km from the Lake Bolshoye. Additionally, in July 2020 and 2021, the Semyonovskoye and Ledovoye lakes located within the city were repeatedly surveyed, but no *R. tridactyla* were recorded there, the same as in previous years (summer seasons of 2000–2019). Thus, during the observation period, the Lake Bolshoye was the only one that attracted kittiwakes in Murmansk vicinity.

The dynamics of the abundance of birds flying during the day followed a bell-shaped curve (Fig. 2). The first flying birds were registered at 9:00, and the last ones, at 18:00; the peak occurred between 12:00 and 14:00, close to noon for Murmansk (12:56). Birds moved along the migration route in both directions simultaneously.

In both years of our observations, there were more birds flying toward the Lake Bolshoye than returning to the Kola Bay. Apparently, this is due to the fact that kittiwakes flew to the lake in organized flocks and tended to return individually choosing their own flyways. As a result, the flight front could widen, and the flow density could decrease. In both years, the proportion of single birds returning from the lake was 2–3 times higher compared to that of kittiwakes flying to the lake.

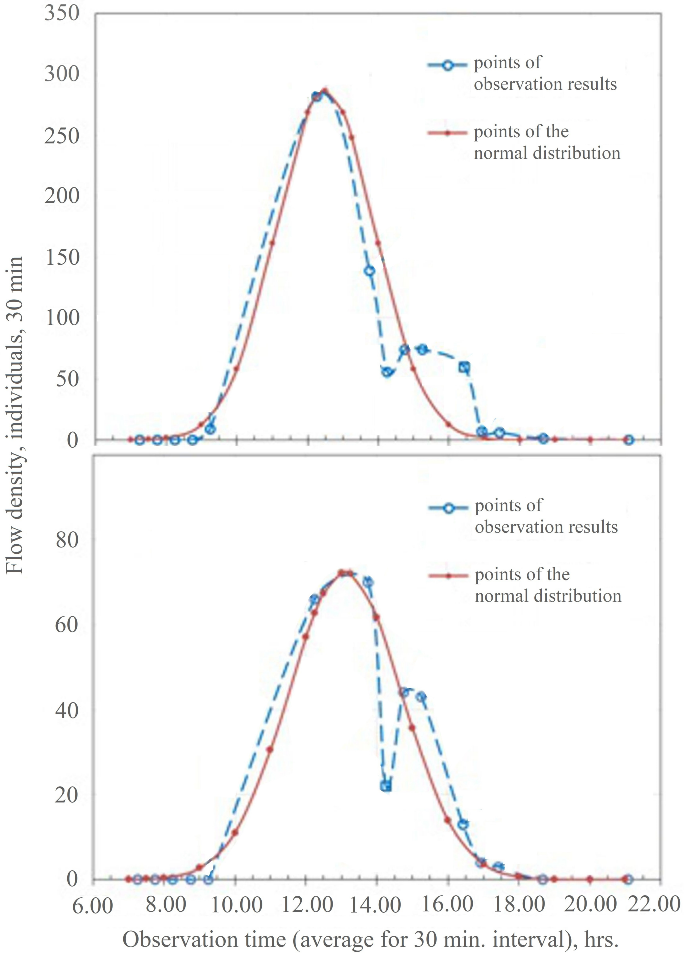

Fig. 2. The results of count observations of birds (2020) flying to the lake (upper diagram) and to the bay (lower diagram); the normal approximation of the observation data. The dots on the dashed line (○) are results of the observations; the dots on the solid line (●) are calculated values of the normal distribution curve

Approximating the daily flow density by a normal distribution for birds flying to the lake, we obtained N = 1,005, with $a \approx 12.50$ (this value corresponds to 12:30 Moscow time) and $\delta \approx 1.4$. For kittiwakes flying to the bay, we had N = 290, with $a \approx 13.10$ (13:06 Moscow time) and $\delta \approx 1.6$.

Considering that some birds flying to the Lake Bolshoye were encountered simultaneously with those returning, it is likely that the total abundance of kittiwakes migrating to the lake and back is around 1,200–1,500 ind.

Flight altitude of birds ranged 10–115 m above the ground. The mean flight altitude differed significantly for two years of our observations. The values were (52.5 ± 2.64) m in 2020 and (40.12 ± 1.65) m in 2021; accordingly, the mean flight attitude decreased by an average of 10 m over the year ($P < 0.001$). In the first year, the straight flyway toward the Lake Bolshoye was frequently interrupted by brief periods of low-altitude circling (noted for 21% of all kittiwakes recorded from the stationary observation point). During the second year, this behavior was registered much less frequently (for 1.5% of birds).

DISCUSSION

Daily migrations to freshwater basins appear to be common for *R. tridactyla* during its breeding season, although their descriptions in scientific literature are rare. In July–August 1996, when carrying out fieldwork authorized by the Kandalaksha State Nature Reserve, A. Goryaeva observed daily flights of kittiwakes from a bird cliff at Cape Krutik (northern coast of the Kola Peninsula) to a small (280 × 140 m) lake (N69.0849°, E35.5693°) located 1 km from the Cape Krutik cliff. Back then, birds flew daily from the cliff to the lake and back ignoring other nearby lakes. Similar migrations of kittiwakes to lakes have been observed in the Svalbard archipelago area. They flew there during the day gathering in flocks up to 200 ind. [Ivanenko, 2012]. According to Yu. Krasnov and N. Nikolaeva [1998], regular occurrence of kittiwake flocks in areas of the Kharlovka River mouth and freshwater lakes on the Kharlov Island (Eastern Murman) is an important element of the birds' behavior during molting, but it is not associated with their feeding activity. When moving toward the river mouth, kittiwakes form flocks resembling a winding ribbon and occasionally stretching over 1 km in length. V. Modestov called the Kharlovka River mouth, where he observed large aggregations of *R. tridactyla*, their favored feeding site. There, he documented 1 ind. of a small trout *Salmo trutta* in a kittiwake's stomach [Modestov, 1967]. Although this bird relies entirely on marine-derived food (fish, crustaceans, and molluscs) [Belopolsky, 1957], its foraging territories on the mainland coast also cover inland sites, including tundra lakes and rivers [Kuklin, 2013]. When occurring in such biotopes, *R. tridactyla* become infected with freshwater helminths, and this evidences for their foraging activity in these freshwater systems [Kuklin, 2013].

A directed flight of gulls is not widely discussed in literature. N. Tinbergen [1974] distinguishes the following types of a directed flight for the European herring gull: a flight to a roosting site, a return from the sea to the breeding colony, and a flight to a feeding site. This researcher considers migration to be an extreme case of a directed flight differing only quantitatively from a flight to a roosting site, a return from the sea to the breeding colony, or a flight to a feeding site. V. Dolnik, in his fundamental work "Migratory State of Birds" [1975], identifies the following types of bird movements: daily migrations between feeding and resting sites, shifts in habitats due to changes in food availability or population density, dispersal for settlement, invasions as the expulsion of excess individuals beyond the species range, and regular seasonal migrations. Based on V. Dolnik's classification, we can conclude that this case most likely represents "a daily migration between feeding and resting sites."

The kittiwake breeds in dense colonies on steep cliffs along sea coasts forming so-called bird cliffs [Belopolsky, 1957].

The first evidence of *R. tridactyla* breeding in the Kola Bay dates back to 1999. Since then, there was a small breeding colony (about 50 pairs in 1999) on a floating dock near southern piers of the commercial port. In 2004, its population reached approximately 200 pairs. In the 2000s, there was a small colony of kittiwakes (50–60 breeding pairs) on walls of a dock in the inner harbor of the Roslyakovo village (middle section of the Kola Bay). In 2009, the dock was sunk; *R. tridactyla* moved to the mainland coast of the harbor and established a colony. In the summer of 2010, 75–80 pairs of birds bred there. Also, kittiwakes breed in small colonies in the northern Kola Bay; the largest and most stable colony (at least 100–200 pairs) is located on the eastern shore of the Pala Bay. In summer, *R. tridactyla* periodically occur in high abundance in the northern Kola Bay pursuing schools of small pelagic fish [Krasnov, Goryaev, 2013].

Unlike large gulls, the European herring gull and sea gull which have been breeding in the residential area of Murmansk for many years [Goryaeva, 2007, 2013], the kittiwake has not been encountered in the city or on nearby lakes since 1998 [Kharlamova, Novikov, 2019]. According to A. Goryaeva, *R. tridactyla* was not observed during bird surveys in Murmansk in 2000–2019 (approximately 300 km of survey routes *per* year in the residential part of the city). Moreover, at the spots where kittiwakes were recorded in 2020 (the flight route over the city center), A. Goryaeva had been carrying out annual summer observations of breeding European herring gulls since 2005, and no kittiwakes have been previously noted. The Kola Bay shores are under much anthropogenic load since the late 1990s; apparently, because of the fact that *R. tridactyla* breed there, birds became able to fly over Murmansk by 2020.

Synanthropic tendencies in the behavior of the kittiwake are not observed everywhere. In literature, there are no mentions of the presence of this species in residential areas of Russian cities. Foreign publications report cases of the kittiwake breeding in cities in the UK and Norway [Nilsen, 2020; Turner, 2010].

The combination of the kittiwake's choice of man-made structures for breeding (synanthropization) and its occurrence on freshwater basins has been described for the River Tyne area (the North East England) [Coulson, MacDonald, 1962; Temperley, 1951; Turner, 2010]. Kittiwakes were not encountered on the River Tyne until 1951; that year, a single bird was registered [Temperley, 1951]. Over the next decade, the situation changed significantly, and by 1961, *R. tridactyla* could be seen almost every day February to June within sight of the bridge over the River Tyne. During this period, most kittiwakes noted on the river were foraging – picking up food from the water's surface [Coulson, MacDonald, 1962]. Moreover, birds gathered to feed near sewage outflows. In the same years, on the freshwater River Derwent (17 km inland from the coast of England) which flows into the River Tyne, kittiwakes fed almost exclusively on fish sometimes reaching 6 inches (15 cm) in length (its species was not identified). According to [Coulson, MacDonald, 1962], kittiwakes tend not to fly over land, except when they gather to bathe in freshwater or, in High Arctic, when they migrate to inland nesting cliffs and back. By 1961, these birds began visiting a freshwater lake in a park in South Shields (a town on the right bank of the River Tyne). Initially, they came to this lake just to bathe, but after five years, they started feeding on bread thrown to other birds – the black-headed gull *Larus ridibundus* and mute swan *Cygnus olor*. By 1961, kittiwakes were regularly flying over the center of North Shields (a town on the left bank of the River Tyne) to a small reservoir in the town center, approximately 1.5 miles from the coast. After visiting the lake, these birds rested on a parapet of a nearby church. In 1962, J. Coulson noted for the first time that *R. tridactyla* was likely feeding regularly on fish caught in freshwater and more and more often feeding on bread. The researcher suggested as follows: in the coming years, this bird might be more frequently observed in freshwater during its breeding season. By 1962, the kittiwake was resting on buildings along the River Tyne leading J. Coulson to predict the establishment of breeding colonies there. His expectations were fulfilled in the subsequent years. *R. tridactyla* breeding colonies began to appear on walls of buildings along the River Tyne and accounted for 450–550 pairs within 1995–2005 and 755 pairs in 2007 [Turner, 2010]. Thus, in this region, manifestations of synurbization cover the occurrence of birds in urban spaces and their visits to freshwater basins in anthropogenic landscapes.

For the kittiwake flying over Murmansk, a decline in flight altitude over the city in the second year of the migration route existence can presumably be considered as the fact of birds becoming accustomed to the urban environment. This is supported by the reduction in circling behavior during flight in the second year.

Some questions arise regarding *R. tridactyla* selectivity in choosing the Lake Bolshoye, as kittiwakes were recorded only on this lake within the city and its immediate vicinity. According to other Murmansk researchers [Kharlamova, Novikov, 2019], during surveys on birds visiting the Lake Bolshoye, no *R. tridactyla* were registered there between 1998 and 2019. As reported in [Zubova et al., 2021], in 2020, in the Lake Bolshoye, *S. trutta* occurred, 149–233 mm in length (the species previously found by V. Modestov [1967] in a kittiwake's stomach in the Kharlov Island area), along with the vendace *Coregonus albula* and three-spined stickleback *Gasterosteus aculeatus*. For comparison: from the Lake Semyonovskoye, only two fish species were reported, the European perch *Perca fluviatilis* and northern pike *Esox lucius*; in the Lake Ledovoye, no fish were caught [Zubova et al., 2021], likely due to its severe pollution. Thus, the ichthyofauna of the Lake Bolshoye meets dietary requirements of the kittiwake. Although foraging is not the primary aim of the bird's visits to freshwater basins [Krasnov, Nikolaeva, 1998], the availability of food seems to play a determining role in *R. tridactyla* choice of lakes.

Conclusions:

- In 2020, a daily migration route of a seabird, the kittiwake *Rissa tridactyla*, was registered over the residential part of Murmansk for the first time.
- The daily dynamics of the abundance of flying birds followed a normal distribution curve occurring between 9:00 and 18:00, with a peak at 13:00–14:00.
- The abundance of *R. tridactyla* flying through the center of Murmansk in July–August 2020–2021 reached 1,500 ind. *per* day, with a flyway width of about 300 m.
- The behavior of the birds in the first year of the migration route's formation differed slightly from that in the following year in terms of flight patterns and altitude.
- The kittiwakes' visits to the Lake Bolshoye may be related to bathing in freshwater and feeding there during the breeding season.

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ПЕРВЫЕ ЛОКАЛЬНЫЕ ПЕРЕМЕЩЕНИЯ МОЕВКИ *RISSA TRIDACTYLA* (LINNAEUS, 1758) НАД ЖИЛЫМИ КВАРТАЛАМИ ГОРОДА МУРМАНСКА

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Во всём мире регистрируют новые проявления синантропных тенденций у разных видов птиц. В данной работе описано появление моевок в городе Мурманске. Проведено наблюдение за впервые сформированным в 2020 г. маршрутом летней суточной миграции *Rissa tridactyla* через центр Мурманска, где этот вид ранее не встречали. Определены некоторые особенности пролёта в первый (2020 г.) и второй год (2021 г.) существования маршрута. Установлена приблизительная численность пролетающих птиц — до 1500 особей в сутки. Появление этого вида активности птиц можно считать первым этапом в освоении моевкой жилой части города.

Ключевые слова: моевка, *Rissa tridactyla*, город, озеро

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ABNORMAL DECREASE IN ABUNDANCE AND BIOMASS OF POPULATION OF *CALANUS EUXINUS* (COPEPODA) IN THE DEEP-SEA AREAS OF THE BLACK SEA IN AUTUMN 2019: WHAT IS HAPPENING WITH THE ECOSYSTEM?

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During plankton sampling in deep and shelf areas of the Black Sea off the Crimea in October 2019 (the 110th cruise of the RV "Professor Vodyanitsky"), the quantitative distribution, abundance, biomass, size and age structures, and lipid reserves of *Calanus euxinus* Hulsemann, 1991 population were studied. Zooplankton was sampled with the Bogorov–Rass net (inlet area of 0.5 m^2, and mesh size of 300 μm) by vertical net hauls from the bottom or the lower boundary of the oxygen zone to the sea surface. Size and age of *C. euxinus* were determined under a stereomicroscope in a laboratory. Lipid reserves in the population were estimated based on the specific oil sac volume at the late copepodite stages. As shown, in 2019, ongoing warming in the Sea of Azov–Black Sea region led to a decrease in *C. euxinus* abundance and biomass in deep-sea areas down to (5.3 ± 0.5) thousand ind.·m^{-2} and (3.7 ± 0.3) g·m^{-2}, respectively, and also to changes in the population structure. Partly, these phenomena could be related to a weakening of winter convective mixing in the sea. Probably, a drop in river inflow after severe drought in 2018–2019 was even more important for *C. euxinus*, as it dramatically reduced the supply of nutrients to the sea. Due to a weak transfer of nitrates, phosphates, and especially silicates with the river flow, abundant phytoplankton (first of all, diatoms critically needing silicates) had insufficient mineral sources for its development in 2019 and, correspondingly, could not satisfy *C. euxinus* trophic requirements at the level of previous years. An increase in lipid content of V copepodites in autumn 2019 is explicable by an abnormally low density of *C. euxinus* population that year driven, apparently, by an extremely high biomass of planktivorous jellyfish, especially the medusa *Aurelia aurita* Linnaeus, 1757, in winter–spring 2017–2018.

Keywords: *Calanus euxinus*, abundance, biomass, lipid reserves, interannual dynamics, Black Sea

A copepod *Calanus euxinus* Hulsemann, 1991 is a key mesozooplankton species in the Black Sea constituting 60–75% of its total biomass, or 76–85% of crustacean plankton biomass in deep-sea areas [Anninsky, Timofte, 2009; Arashkevich et al., 2014; Zagorodnyaya et al., 2023]. This species is the largest Black Sea copepod: females can reach 4.5 mm in length, and males attain 3.4 mm [Sazhina, 1987]. *C. euxinus* features high wax content (up to 40% of its body volume) [Yuneva et al., 1999] accumulated primarily in late copepodites and adults within an oil sac. Because of these lipid reserves, some individuals can possess a reddish coloration. Due to its visibility, high nutritional value, and tendency to form localized aggregations, *C. euxinus* is critically important for the diet of small pelagic fish, particularly the cold-water Black Sea sprat *Sprattus sprattus phalericus* (Risso, 1827) which mostly consumes large cold-water zooplankton [Bayhan, Sever, 2015; Latun, 2014; Yuneva et al., 2016].

C. euxinus can produce up to eight generations annually [Sazhina, 1987] maintaining its biomass at relatively stable levels, with slight increases in spring and declines in winter [Vinogradov et al., 1999]. In the 1970–1980s, its biomass in open sea areas averaged 5–10 $g \cdot m^{-2}$. However, following the invasion of the lobate comb jelly *Mnemiopsis leidyi* (A. Agassiz, 1860), biomass of the copepod decreased to 1–3 $g \cdot m^{-2}$ in the Black Sea in 1991–1992 [Kovalev, 1996; Vinogradov et al., 1999]. By October 2005, *C. euxinus* biomass in the western deep-sea area had risen again to 6.2 $g \cdot m^{-2}$ [Anninsky, Timofte, 2009]. In the autumn of 2016 and 2017, at the sites to the south of the Crimea, it reached 7.1 and 7.3 $g \cdot m^{-2}$, respectively [Hubareva, Anninsky, 2022, 2024].

Significant interannual fluctuations in mesozooplankton abundance and biomass on the Black Sea shelf [Anninsky et al., 2020; Gubanova et al., 2022] evidence for the fact that populations of the copepod are not only vulnerable to planktivorous jellyfish invasions, but also dependent on hydrological regime shifts. Over the last decades, the annual mean surface temperature of the Black Sea was rising by 0.052 °C *per* year [Ginzburg et al., 2021]. Oxygen penetration depth in the sea decreased from 140 m in 1955 to 90 m in 2015, with total oxygen content declining by 44% [Capet et al., 2016]. Stagnation processes in the sea [Polonsky, Valle, 2020; Vidnichuk, Konovalov, 2021] disrupt vertical migrations and lipid formation in cold-water crustaceans, particularly *C. euxinus*, with its major population remaining constantly in diapause near the lower oxycline boundary [Vinogradov et al., 1992].

In 2019, an autumn study of *C. euxinus* abundance, biomass, distribution, size and age structures, and lipid reserves of the Black Sea population extended investigations carried out in 2016 and 2017 [Hubareva, Anninsky, 2022, 2024]. The survey was aimed at assessing the species response to regional climate warming and associated recent hydrological changes in the sea.

MATERIAL AND METHODS

In autumn 2019 (7–21 October, the 110th cruise of the RV "Professor Vodyanitsky"), zooplankton was sampled in the Black Sea, at 69 stations covering deep-sea and shelf areas southwest, south, and southeast of the Crimea, in a sector from N43°02′ to N44°59′ and from E32°10′ to E38°40′ (Fig. 1). Three stations were situated in the inner shelf zone (depths < 50 m), and ten were located on the outer shelf (depths 50–200 m). Deep-sea stations were classified by their hydrological regime into cyclonic gyre cores, with an isopycnal depth ($\sigma_t = 16.2$) of < 125 m (18 stations); cyclonic peripheries, with a depth of 126–150 m (31 stations); and anticyclonic eddies, with a depth of > 150 m (7 stations) (Fig. 2).

Prior to plankton sampling, hydrological measurements were conducted at each station with a research tool Sea-Bird 911 plus CTD (the USA) to assess vertical profiles of temperature, salinity, and seawater conditional density (σ_t). Zooplankton was quantitatively sampled with a Bogorov–Rass net (inlet area of 0.5 m^2, mesh size of 300 μm) by total vertical hauls from the seabed or the lower boundary of the oxygen zone ($\sigma_t = 16.2$) to the sea surface. Samples containing *C. euxinus*, including copepodite developmental stages and adults, were preserved in a 4% borax-neutralized formalin solution. Subsequent laboratory processing involved examining the samples in a Bogorov chamber under a stereomicroscope to measure and identify *C. euxinus* developmental stages. Population structure was typically assessed by full examination of the entire sample. However, when late developmental stages were abundant, they were quantified *via* subsampling [Alexandrov et al., 2020]. Reserve lipid content in *C. euxinus* was evaluated based on oil sac volume in V copepodites, males, and females. Corresponding measurements were carried out for 20 ind. *per* certain developmental stage at each station.

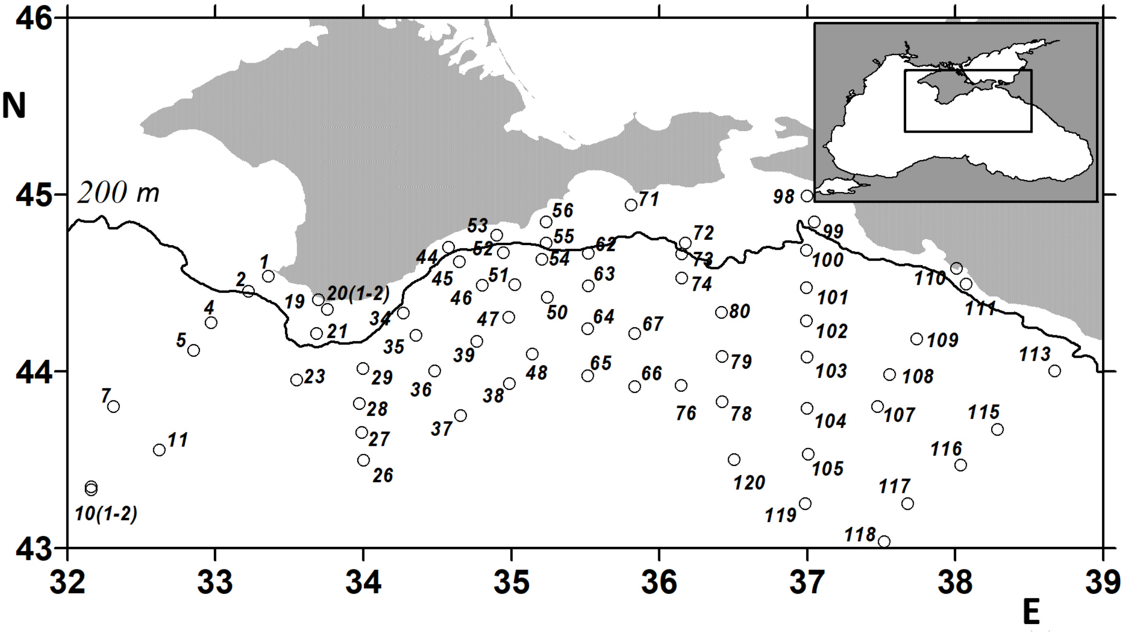

Fig. 1. The map of sampling survey (with station numbers identified) in the northwestern, central, and northeastern Black Sea during the 110th cruise of the RV "Professor Vodyanitsky" in October 2019. The line shows the 200-m isobath

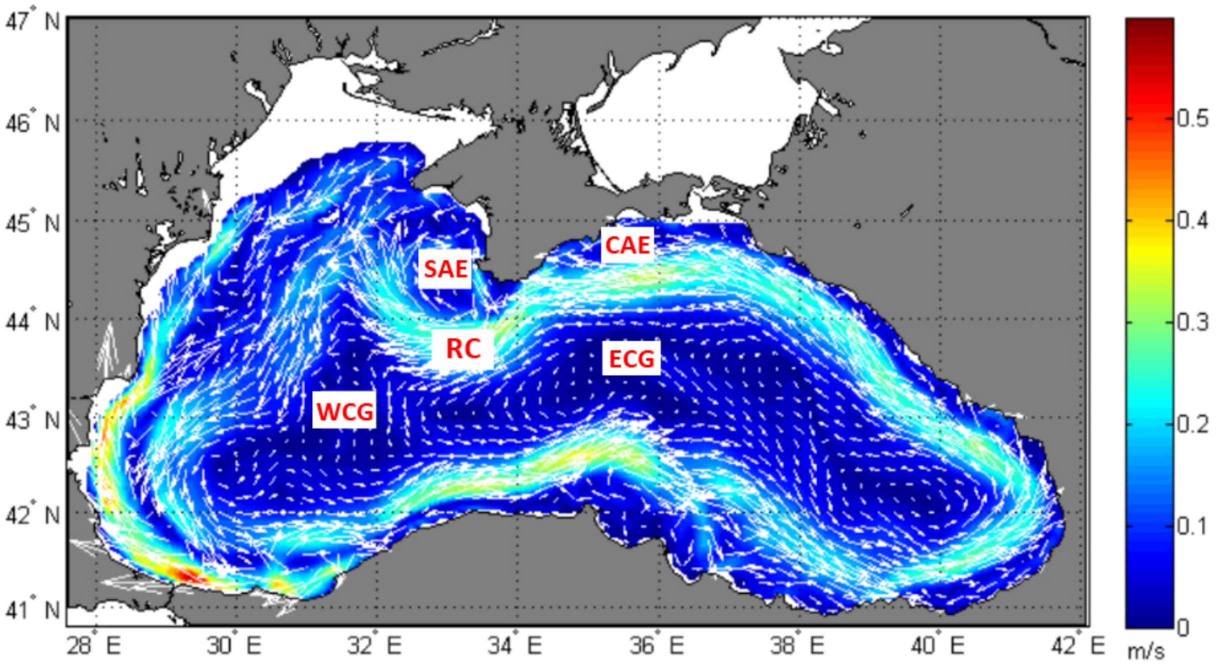

Fig. 2. Hydrodynamic activity in the Black Sea at a 30-m depth from 15 October to 15 November, 2019 (https://dekosim.ims.metu.edu.tr/BlackSeaModels/BlackSeaModels.shtml). RC, the Rim Current; WCG, the Western Cyclonic Gyre; ECG, the Eastern Cyclonic Gyre; SAE, the Sevastopol Anticyclonic Eddy; CAE, the Crimea Anticyclonic Eddy

The individual wet weight of copepodites and adult *C. euxinus* (WW, mg) was calculated by the formula:

$$WW = 0.58 \times l \times d^2 \times \rho \,,$$

where l and d are prosome length and width, respectively, mm;

ρ is a mean body density, g·cm^{-3} [Svetlichny, Hubareva, 2014].

The body volume of copepodite stages, males, and females (V_b, mm^3) was determined using the formula:

$$V_b = k \times L_{pr} \times d_{pr}^2 \,,$$

where L_{pr} and d_{pr} are prosome length and width, respectively, mm;

k is an empirical coefficient equal to 0.64 for males and 0.58 for copepodites and females [Svetlichny et al., 2009].

The oil sac volume (V_{sac}) was calculated as:

$$V_{sac} = \pi \times l_{sac} \times d_{sac}^2 / 6 \,,$$

where l_{sac} and d_{sac} are oil sac length and width, respectively, mm [Svetlichny, Hubareva, 2011].

Data were processed in MS Office Excel 2010, Grapher 7, PAST 4.05 [Hammer et al., 2001], and Surfer. In all cases, means and corresponding values of a standard error (±*SE*) are provided. Differences between analyzed datasets were assessed using Student's *t*-test and non-parametric Mann–Whitney *U* test.

RESULTS

Hydrological conditions in the study area. Within the survey period, sea surface temperature ranged from +15.6 to +20.4 °C, with the mean of (+18.4 ± 0.1) °C. It was slightly lower in central deep-sea areas south of the Crimean Peninsula (Fig. 3).

In this area, the temperature field evidences for a significant upwelling of cold deep waters to the surface, and this is likely associated with hydrodynamic instability on the periphery of the Eastern Cyclonic Gyre. This was further supported by a concurrent increase in surface water salinity at the survey site. In the western study area, salinity varied within 18.28–18.62 psu, with the mean of (18.4 ± 0.02) psu. In the eastern study area, the range was wider, 17.37–19.36 psu, with the mean of (18.6 ± 0.1) psu. The lowest salinity values, 17.37–18.27 psu, were recorded at sta. 72 and 73 resulting from the inflow of freshened Sea of Azov water into the Kerch pre-strait.

The lower boundary of the upper quasi-homogeneous layer corresponding to the upper thermocline boundary was located at similar depths in the western and eastern deep-sea areas: at 11–36 m [the mean of (21.0 ± 1.0) m] and 14–34 m [the mean of (20.0 ± 1.4) m]. In both cases, the thermocline depth was mainly mediated by mesoscale water circulation. Thus, thermocline raises in cyclonic circulation zones (south of the Cape Chersonesus, sta. 23) and deepens within cores of anticyclonic eddies, with Sevastopol and Crimean anticyclones being especially notable.

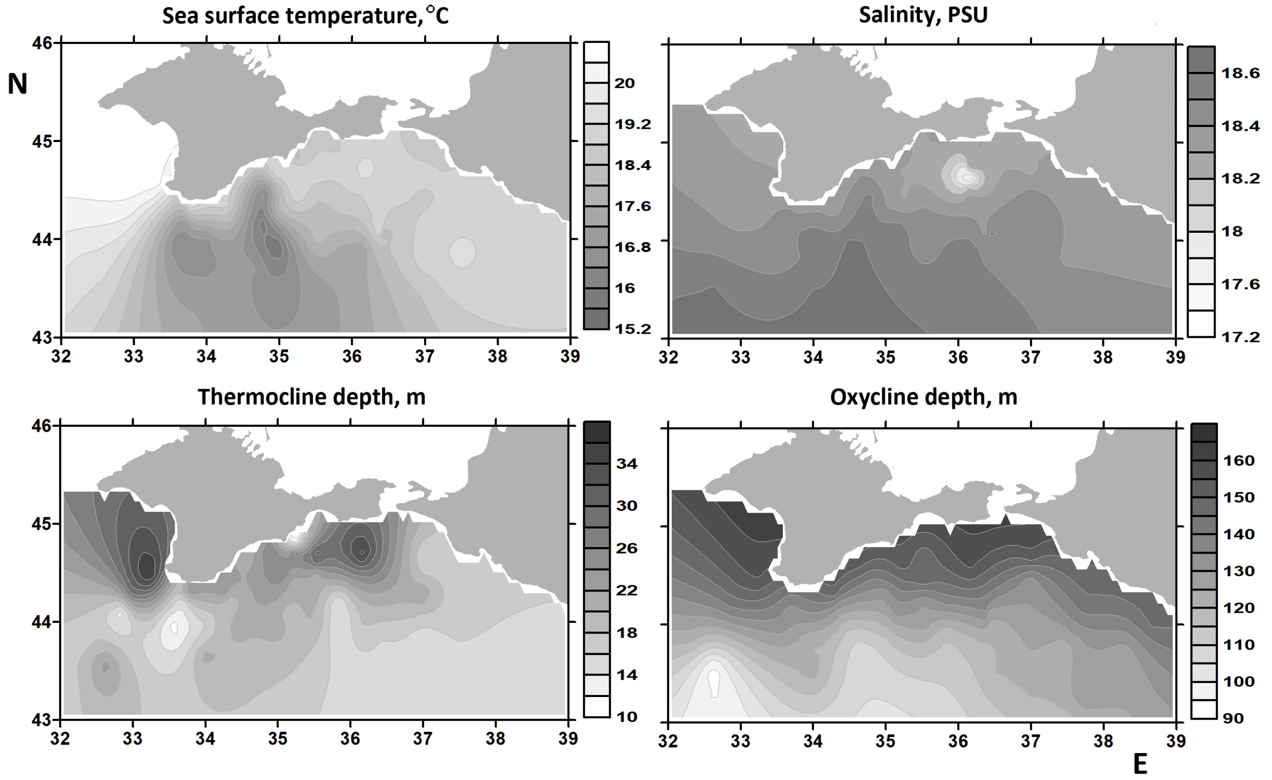

Fig. 3. Spatial distribution of temperature (°C) and salinity (psu) in the sea upper layer, as well as depths (m) of the upper boundary of the thermocline and the lower boundary of the oxygen zone in the Black Sea on 7–21 October, 2019

Quantitative distribution of *Calanus euxinus*. Its maximum abundance (21.2 thousand ind.·m^{-2}) and biomass (15.3 g·m^{-2}) in October 2019 (Fig. 4) were recorded in the cyclonic meander zone of the Rim Current identified by the relatively shallow thermocline depth and localized sea surface temperature decrease (sta. 23) (see Fig. 3). However, no statistically significant correlation was found between the species biomass and hydrodynamic phenomena in the deep-sea area, although its total abundance gradually rose with the deepening of the lower boundary of the oxygen zone (hereinafter LBOZ) ($r = 0.32$; $p < 0.05$). *C. euxinus* mean biomass slightly increased from central areas of cyclonic gyres [(3.2 ± 0.3) g·m^{-2}] toward their peripheries [(4.2 ± 0.5) g·m^{-2}], but decreased [(2.9 ± 0.4) g·m^{-2}] with LBOZ deepening to 150–160 m. Abundance values followed this trend accounting for (3.7 ± 0.4), (6.2 ± 0.7), and (5.8 ± 1.1) thousand ind.·m^{-2} (in the same sequence). A slight gain in the species abundance with LBOZ deepening was governed by higher abundance of early copepodite stages which develop in warmer waters displaced toward gyre peripheries by centrifugal currents.

In deep-sea areas, *C. euxinus* abundance and biomass were (5.3 ± 0.5) thousand ind.·m^{-2} and (3.7 ± 0.3) g·m^{-2}, respectively. On the outer shelf, the values decreased to (4.8 ± 1.1) thousand ind.·m^{-2} and (1.5 ± 0.5) g·m^{-2}. A significant (2.5-fold; $p < 0.001$) decline in biomass of this copepod reflects the dominance of early developmental stages in shallow waters. On the inner shelf, its abundance and biomass were even lower: (2.2 ± 1.5) thousand ind.·m^{-2} and (0.3 ± 0.3) g·m^{-2}, respectively.

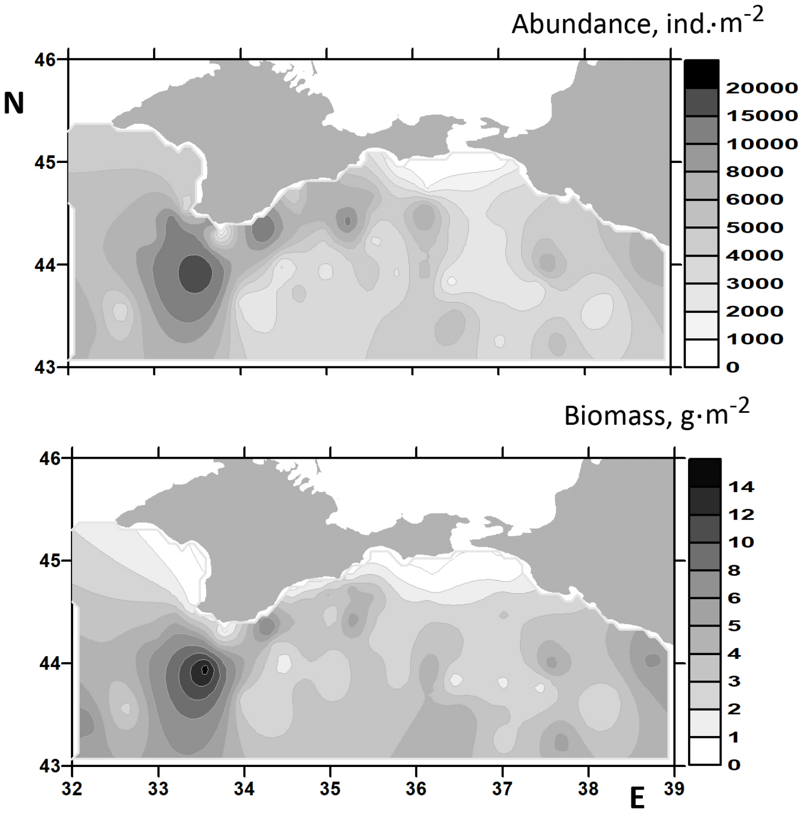

Fig. 4. Abundance and biomass of a copepod *Calanus euxinus* in the northwestern, central, and northeastern Black Sea in October 2019

Age structure of *Calanus euxinus* population. The population structure was mediated by features of hydrodynamic conditions (Fig. 5). In central cyclonic gyres, proportions of V copepodites [(49.5 ± 4.1) %] and females [(33.1 ± 3.2) %] were 1.5–2 times higher than in anticyclonic eddies [(31.4 ± 2.4) and (15.9 ± 4.5) %, respectively]. Proportions of I–III and IV copepodites increased inversely: from (6.2 ± 1.3) % and (2.2 ± 0.4) %, respectively, at LBOZ of 100–125 m to (35.3 ± 5.0) % and (10.5 ± 2.4) % at LBOZ of 150–160 m. The relative abundance of males varied between 6.7 and 10.5%.

On the outer shelf, the proportion of I–III copepodites increased to (64.8 ± 7.8) %, while proportions of V copepodites, females, and males dropped to (13.2 ± 3.1), (9.3 ± 4.0), and (2.8 ± 0.9) %, respectively. The numerical prevalence of early developmental stages in *C. euxinus* population became even more pronounced on the inner shelf: there, I–III copepodites constituted (89.0 ± 2.1) %, while V copepodites and adults occurred singly in autumn.

Lipid reserves of *Calanus euxinus* population. Late copepodite stages exhibited higher reserve lipid content in deep-sea areas, where the oil sac volume relative to body volume reached (24.0 ± 0.7) % in V copepodites, (7.0 ± 1.1) % in females, and (11.5 ± 0.5) % in males. Interestingly, in central cyclonic gyres, V copepodites, females, and males accumulated much more lipids than in peripheral areas [(25.7 ± 1.2), (9.7 ± 1.2), and (13.1 ± 0.8) %, respectively], though these differences were not statistically significant ($p > 0.05$). On the outer shelf, V copepodites stored half lipid reserves of those in open sea areas [(11.9 ± 1.7) %; $p < 0.001$]. However, the mean oil sac volume in females and males [(6.3 ± 0.8) and (8.0 ± 1.4) %, respectively] remained the same ($p > 0.05$).

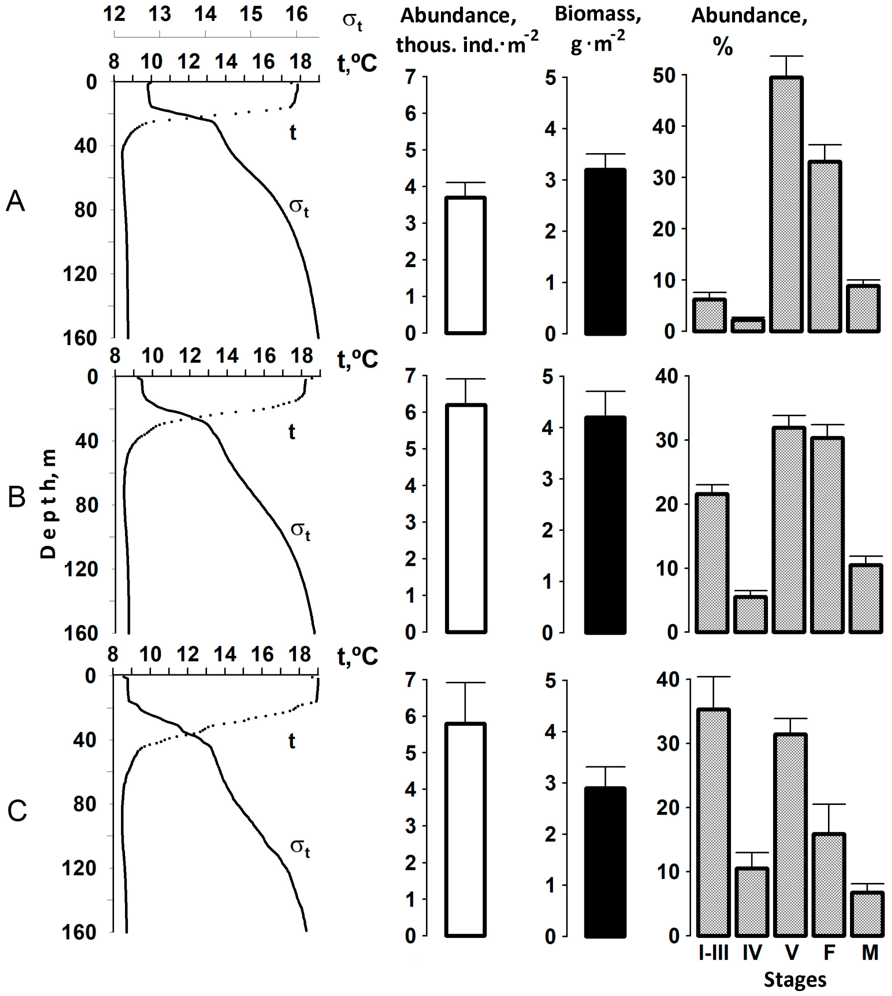

Fig. 5. Total abundance (thousand ind.·m^{-2}), biomass (g·m^{-2}), and age structure (% of total abundance) in *Calanus euxinus* population in relation to vertical profiles of seawater temperature (t, °C) and density (σ_t) in deep-sea areas of the Black Sea. The depth of the lower boundary of the oxygen zone (σ_t = 16.2): 100–125 m (A); 126–150 m (B); 151–160 m (C)

DISCUSSION

In deep-sea areas, *C. euxinus* biomass in October 2019 was nearly twice as low ($p < 0.001$) as during autumn of 2016 and 2017 [Hubareva, Anninsky, 2022, 2024]. Furthermore, it was significantly lower ($p < 0.05$) than biomass of this species in 2005 [Anninsky, Timofte, 2009], when mesozooplankton community seemed to be still recovering from the damage caused by the invader *M. leidyi*. Biomass of this copepod declined most sharply in central cyclonic circulation zones ($p < 0.001$) and on their peripheries ($p < 0.001$ in 2016; $p < 0.05$ in 2017). Even in areas of surface water downwelling, *C. euxinus* biomass was 2–2.5 times lower compared to that in 2016 and 2017, though high data variability in the first case precluded statistical significance ($p > 0.05$). On the outer shelf, a twofold biomass decline was also statistically unsignificant ($p > 0.05$).

In general, interannual changes in abundance of this copepod were similar to dynamics of its biomass. However, on the periphery of cyclonic gyres, in 2019, compared to 2016 and 2017, a decrease in *C. euxinus* abundance was 10–20% less intense than a decline in its biomass. In anticyclonic deep-sea areas, the difference reached 30–40%. This suggests that negative changes in the copepod population in 2019 had effect on the late developmental stages, that dominate in terms of contribution to biomass. At the same time, early copepodites which are more critical for abundance assessment, mostly preserved their stable level in plankton.

The analysis of *C. euxinus* population structure revealed that the proportion of I–III copepodites in deep-sea areas gradually increased: from 5.7% in 2016 to 17.6% in 2017 and 21.0% in 2019. This tendency was driven by a rise in their proportions in anticyclonic deep-sea areas, where these stages accounted for 12.2% of total abundance in 2016, 16.1% in 2017, and 35.3% in 2019. Concurrently, the proportion of V copepodites declined gradually from 48.2 and 35.7% in 2016 and 2017 to 31.4% in 2019. The same shifts were observed in females (from 27.7 and 25.3% to 15.9%).

Despite reduced abundance and biomass of V copepodites in 2019, their lipid reserves increased (Fig. 6). The oil sac volume in these copepodites rose compared to that in 2016–2017 under different hydrological regimes: in central cyclonic zones (from 16.6 and 17.2% to 23.7%), on gyre peripheries (from 16.6 and 18.7% to 24.4%), and in the zone of anticyclonic eddies (from 17.4 and 18.6% to 23.7%). No noticeable interannual changes were registered in *C. euxinus* female or male lipid reserves suggesting heterogeneity in their reproductive readiness. In contrast, much more elevated lipid reserves in V copepodites in 2019 seem to evidence for the proximity to final metamorphosis and their high reproductive potential upon maturation. Increased lipid reserves imply better feeding conditions in 2019 compared to those in 2016–2017 [Hubareva, Anninsky, 2022, 2024]. This appears to result from a more than twofold reduction in population size in 2019 compared to that in 2016–2019 and a corresponding weakening of intra-population competition for food.

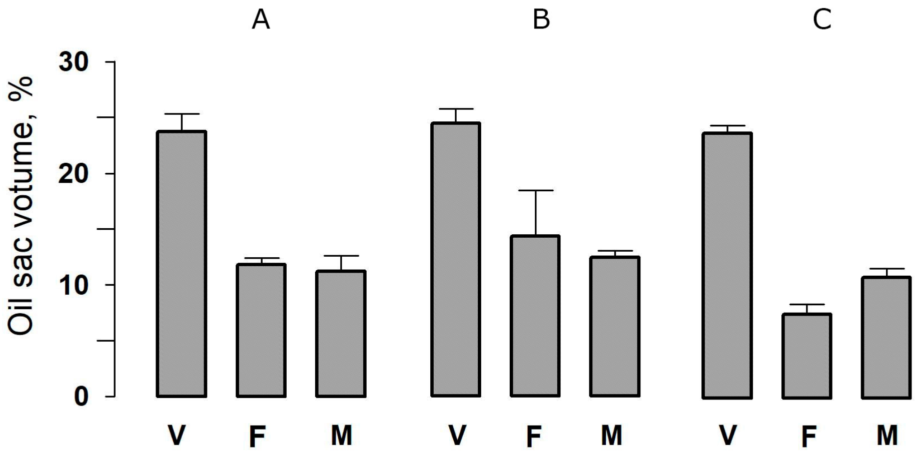

Fig. 6. Specific oil sac volume (% of body volume) in V copepodites (V), females (F), and males (M) of *Calanus euxinus* from the Black Sea areas with different depths of the lower boundary of the oxygen zone (σ_t = 16.2) in October 2019: 100–125 m (A); 126–150 m (B); 151–160 m (C)

Thus, the most distinctive features of *C. euxinus* population in 2019 are as follows:

1) a significant decline in abundance and biomass;
2) structural population shifts mainly mediated by a greater representation of juveniles and a decline in abundance of older age stages;
3) increased reserve lipid content in V copepodites.

The exact reasons of these changes remain unclear, the same as their temporal dynamics. However, several key factors undoubtedly affected both the Black Sea pelagic biota in general and *C. euxinus* population in particular in 2017–2019.

Within 2017–2019, the mean annual temperature in the Black Sea increased by approximately 2 °C. The winter of 2017/2018 was warmer than usual, while the winter of 2018/2019 was exceptionally warm, with air temperature 2.7 °C above the norm [Ginzburg et al., 2021]. This warming not only slowed the seasonal cooling of the sea surface, but also maintained temperature at least 1 °C higher in the core of the cold intermediate layer and within the main pycnocline zone. Convective mixing of water masses during winter significantly weakened, and this, combined with a rise in temperature, contributed to formation of stagnant conditions near LBOZ [Polonsky, Valle, 2020]. Oxygen content in the oxycline layer ($\sigma_t = 15.4$) halved, the upward transport of nitrates from the main pycnocline to the upper layers slowed, and the intensity of spring phytoplankton bloom declined [Vidnichuk, Konovalov, 2021]. The winter–spring phytoplankton peak which usually occurred in February has not been noted at all in recent years [Stelmakh et al., 2023] or was observed in coastal areas alone [Vostokov et al., 2019].

These hydrological shifts projected across the entire pelagic biota and inevitably affected *C. euxinus* population by narrowing boundaries of its oxygenated biotope and reducing the supply of nutrients to the zone of active photosynthesis. However, the effect of spring phytoplankton bloom on this copepod appears to be secondary due to the short duration of this process or the small size of algal cells proliferating during this period [Silkin et al., 2022] and possessing low nutritional value for large copepods [Amelina et al., 2017].

A positive correlation ($r = 0.81$; $p < 0.01$) was observed between *C. euxinus* biomass on the outer shelf of the Sevastopol Bay in 2003–2021 and the sea surface temperature in April and May [Anninsky et al., 2020]. It highlights strong dependence of *C. euxinus* population on regional climate features, particularly in winter and spring. The prevalence of cyclonic atmospheric circulation was characterized by early warming, increased precipitation, and elevated river inflow into the Black Sea [Oguz et al., 2006]; this contributed to greater productivity of the copepod population. This is likely driven by intensified spring flow from rivers, such as the Danube and Dnieper: those account for over 70% of total freshwater inflow to the Black Sea peaking in April and May [Ivanov, Belokopytov, 2011]. Strong floods enhance nutrient enrichment in the pelagic zone and thus form favorable trophic conditions for the copepod providing improved summer–autumn development of large diatoms and phytoplankton in general [Yunev et al., 2021]. Furthermore, chlorophyll *a* anomalies in the upper mixed layer correlate significantly with the Danube inflow across all the Black Sea regions [Nezlin, 2006].

For the Danube basin and the Sea of Azov–Black Sea region, 2018 was one of the driest years in a century [Ginzburg et al., 2021; Hänsel et al., 2022]. Apparently, river flow in 2019 (it was an almost equally low-water year) remained extremely weak [Chasovnikov, Borodulina, 2022]. Such a reduction in freshwater inflow severely limited the supply of nutrients to the sea. Accordingly, concentrations of nitrates, phosphates, and especially silicates in seawater in 2019 were the lowest during the period of observations, at least since 2009 [Chasovnikov, Borodulina, 2022; Orekhova, 2021]. The scarcity of silicates, a critical resource for diatoms, deprived phytoplankton communities of minerals needed for their growth. Consequently, phytoplankton failed to satisfy trophic requirements of *C. euxinus* and other copepods at levels noted in previous years [Datsyk et al., 2020].

How, then, can the high lipid content in V copepodites in 2019 be explained? One of the factors contributing to substantial lipid reserves in *C. euxinus* could be the sparsity of its population (and thus reduced intraspecific competition for food) under limited availability of small diatoms in the sea. It is also possible that gelatinous zooplankton and other planktivores played a certain role. In 2019, *M. leidyi* biomass increased to (144 ± 21) $g \cdot m^{-2}$, and *C. euxinus* occasionally dominated among preys of the lobate comb jelly in deep-sea areas [Anninsky et al., 2024]. However, even more pronounced effect on the copepod population may be related to the extremely high biomass of the common jellyfish *Aurelia aurita* Linnaeus, 1757 in autumn 2017: (514 ± 159) $g \cdot m^{-2}$ on the outer shelf and (634 ± 87) $g \cdot m^{-2}$ in deep-sea areas, that was threefold higher than the long-term mean over 2005–2019 [Anninsky et al., 2022]. The relatively high biomass of *C. euxinus* during autumn study in 2017 does not preclude a sharp decline later that year or in early 2018. Specifically, after the mass development of *M. leidyi* in 1988–1989, a decrease in the copepod biomass became evident only in 1991–1992 [Vinogradov et al., 1999]. The vertical distribution of *A. aurita* population overlapped more with *C. euxinus* populations, than it was typical for *M. leidyi*. Abundance of the copepod might have dropped due to intense predation by the common jellyfish on eggs, early developmental stages, and, in some cases, migrating V copepodites and adults. Apparently, the active accumulation of lipid reserves in *C. euxinus* was facilitated by its ability to feed on large-cell diatoms adapted to inhabit nutrient-poor waters [Stelmakh et al., 2023].

Conclusion. Ongoing warming in the Sea of Azov–Black Sea region led to large-scale transformations in the Black Sea pelagic zone in 2019 causing a sharp decline in abundance and biomass, as well as structural shifts in the population of the key mesozooplankton species, *Calanus euxinus*. While the most of the copepod annual cycle occurs at low temperature near the lower boundary of the oxygen zone, direct thermal effects on its population over the recent years have been minimal. However, even slight deviations in winter sea temperature from a norm significantly degraded the species habitat conditions in 2019. The weakening of winter convective water mixing exacerbated stagnation near the lower boundary of oxygen zone. Oxygen content in the oxycline layer decreased twofold, nitrate flux from the main pycnocline to the upper layers slowed, and the intensity of spring phytoplankton bloom declined. However, a drastic reduction in river inflow due to a severe drought of 2018–2019 was even more crucial for *C. euxinus*: it minimized allochthonous supply of nutrients to the sea. In 2019, content of nitrate, phosphate, and especially silicate was the lowest since at least 2009 due to reduced river inflow. Accordingly, abundant phytoplankton, particularly silicate-dependent diatoms, was deprived of mineral resources for its development in 2019 and failed to satisfy *C. euxinus* trophic requirements at the level of previous years, as well as those of copepods in general. Slightly elevated lipid reserves in V copepodites in 2019 might reflect the anomalous sparsity of *C. euxinus* population in that year, potentially driven by unprecedented high biomass of planktivorous jellyfish, especially *Aurelia aurita*, during winter and spring in 2017–2018.

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АНОМАЛЬНОЕ СОКРАЩЕНИЕ ЧИСЛЕННОСТИ И БИОМАССЫ ПОПУЛЯЦИИ КОПЕПОДЫ *CALANUS EUXINUS* В ГЛУБОКОВОДНЫХ РАЙОНАХ ЧЁРНОГО МОРЯ ОСЕНЬЮ 2019 Г.: ЧТО ПРОИСХОДИТ В МОРСКОЙ ЭКОСИСТЕМЕ?

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В ходе планктонных работ, проведённых в глубоководных районах Чёрного моря и на его шельфе у Крымского полуострова в октябре 2019 г. (110-й рейс НИС «Профессор Водяницкий»), исследовали количественное распределение, численность, биомассу, размерно-возрастную структуру и жировые резервы популяции копеподы *Calanus euxinus* Hulsemann, 1991. Пробы зоопланктона отбирали сетью Богорова — Расса (площадь входного отверстия 0,5 м^2, ячея 300 мкм) методом тотальных вертикальных ловов от дна или от нижней границы кислородной зоны до поверхности моря. Размеры и возраст *C. euxinus* определяли под микроскопом. Содержание запасных липидов в популяции оценивали по удельному объёму жировых мешков у рачков старших возрастных стадий. Установлено, что продолжающееся потепление в Азово-Черноморском регионе привело в 2019 г. к сокращению численности и биомассы *C. euxinus* в глубоководных районах до (5,3 ± 0,5) тыс. экз.·м$^{-2}$ и (3,7 ± 0,3) г·м$^{-2}$ соответственно, а также к изменениям в структуре популяции. Отчасти этому способствовало ослабление зимнего конвективного перемешивания водных масс. Вероятно, ещё более существенным для *C. euxinus* было то́, что из-за сильной засухи 2018–2019 гг. произошло резкое снижение паводкового стока рек, ограничившее до минимума поступление биогенных элементов в море. Вследствие слабого выноса с речным стоком нитратов, фосфатов и особенно силикатов массовый фитопланктон (прежде всего нуждающиеся в силикатах диатомовые водоросли) не имел в 2019 г. минеральных ресурсов для своего развития и, соответственно, не обеспечивал на уровне прежних лет трофические потребности *C. euxinus*. Некоторое повышение жирности V копеподитов осенью 2019 г. объяснимо аномальной разреженностью популяции *C. euxinus* в этом году, обусловленной, возможно, беспрецедентно высокой биомассой желетелых планктофагов и особенно медузы *Aurelia aurita* Linnaeus, 1757 в зимне-весенний период 2017–2018 гг.

Ключевые слова: *Calanus euxinus*, численность, биомасса, запасные липиды, межгодовая динамика, Чёрное море

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EFFECT OF GABA MIMETIC PHENIBUT ON OXIDOREDUCTASE ACTIVITY IN THE BRAIN COMPARTMENTS OF ADULT AND JUVENILE SCORPIONFISH *SCORPAENA PORCUS* LINNAEUS, 1758

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An increase in GABA levels serves to the survival of neurons during hypoxia/anoxia. During ontogenesis, GABA is capable of transforming its mediator function from excitatory to inhibitory. The oxidoreductase activity (MDH, 1.1.1.37; LDH, 1.1.1.27; and catalase, 1.11.1.6) was studied in the brain compartments – the medulla oblongata (MB) and the forebrain, diencephalon, and midbrain (AB) – in juvenile and adult black scorpionfish *Scorpaena porcus* against the backdrop of injection of GABA mimetic phenibut (400 $mg \cdot kg^{-1}$, i. p.). AB structures of juvenile scorpionfish were characterized by an intensity of aerobic metabolism comparable to that of adults. At the same time, an elevated LDH activity in juvenile MB and AB was observed which may serve to increased survivorship at low environmental PO_2. Catalase activity in both age groups was somewhat higher in MB which may be related both to the intensity of oxidative phosphorylation and MB tolerance to injuries during hypoxia. Moreover, catalase activity in the brain of juveniles (especially in AB) was slightly lower than that of adults. Phenibut simultaneously increased MDH and LDH activity in the brain compartments of adult scorpionfish which may be associated with the activation of the malate-aspartate shuttle, with an opposite trend towards the restriction of anaerobic glycolysis in the juvenile brain being mostly pronounced in AB ($p < 0.05$). Simultaneously, phenibut contributed to a rise in catalase activity in all brain compartments, regardless of the age of scorpionfish ($p < 0.05$). Catalase activity was the highest in MB of adult individuals ($p < 0.05$). Apparently, catalase-controlled H_2O_2 level translates the changes in cellular metabolism into a meaningful physiological response by influencing H_2O_2-sensitive ion channels that determine neuronal excitability and modulates GABAergic transmission. Such a mechanism may be involved in the brain maturation, maintain brain resistance to hypoxia, and ensure adaptive processes in juvenile and adult scorpionfish.

Keywords: teleost fish, brain, phenibut, GABA receptors, oxidoreductases

Freshwater and marine aquatic ecosystems are subjected to episodes of hypoxia (dissolved oxygen deficiency) of varying severity, periodicity, and duration. Animals appeal to various ways of adaptation to hypoxia, including physiological and molecular mechanisms, metabolic depression, or intensification of anaerobic glycolysis [Hochachka, Somero, 2002]. In any case, fish survival under hypoxia requires a well-coordinated response to either obtain more O_2 from the hypoxic aquatic environment or limit the metabolic consequences of O_2 deficiency.

The brain is the most actively functioning organ of vertebrates requiring O_2 to produce energy. A significant part of energy consumed by the brain (50–60%) is spent on maintaining ionic gradients and restoring them after depolarization of cell membranes. Under hypoxia, the primary and universal cause of fish death is a violation of ATP homeostasis in the brain, regardless of the general hypoxic tolerance of a particular species [Nilsson, Ostlund-Nilsson, 2008].

Hypoxia- and anoxia-tolerant vertebrates can serve as model organisms in the studies of mechanisms of neuronal cell survival under conditions of O_2 starvation [Little et al., 2021]. A common feature for all groups of hypoxia/anoxia-tolerant animals, as O_2 decreases, is the release of the inhibitory neurotransmitter γ-aminobutyric acid (GABA) [Hylland, Nilsson, 1999; Nilsson et al., 1991] against the backdrop of a relative decrease in the level of excitatory mediator glutamate [Nilsson et al., 1991]. At the same time, GABA is the only inhibitory amino acid in anoxia-sensitive species the level of which increases during hypoxia, while concentrations of glutamate and glutamine, as its precursor, remain unchanged or even rise [Nilsson et al., 1991]. It is assumed that one of the main ways of neuronal survival during hypoxia/anoxia is an increase in GABA level, in particular, providing the suppression of electrical activity and limiting energy consumption [Nilsson et al., 1991]. A feature of GABA is the transformation of its mediator function from excitatory to inhibitory during ontogenesis [Ben-Ari, 2014].

The adaptive capabilities of inhabitants of an aquatic environment with constantly varying levels of O_2 and periodic episodes of hypoxia/anoxia largely depend on the effectiveness of the interaction of aerobic and anaerobic pathways of energy metabolism. Oxidoreductases, malate dehydrogenase (MDH, L-malate: NAD-oxidoreductase, 1.1.1.37) and lactate dehydrogenase (LDH, L-lactate: NAD-oxidoreductase, 1.1.1.27), are directly involved in energy production, regulate the redox potential of cells, and serve as markers of the oxidative and glycolytic capacity of energy metabolism. About 90% of MDH activity is localized in the cytoplasm, and only 10%, in mitochondria. The involvement of cytosolic MDH in the transport of NADH equivalents across the mitochondrial membrane allows it to control the format of the tricarbonic acids (TCA) cycle pool size. LDH takes part in the anaerobic fermentation of the end product of glycolysis, *i. e.*, in the reversible pyruvate-to-lactate conversion in cytosol in the absence of O_2, being the terminal enzyme of anaerobic glycolysis. Any change in O_2 intake causes shifts between aerobic and anaerobic pathways of energy metabolic processes oxidoreductases are involved in. The reactions of glycolysis provided by oxidoreductases are an integral part of the mechanism of adaptation to hypoxia.

Disturbances in normal O_2 metabolism in cells lead to enhanced generation of reactive oxygen species (hereinafter ROS) the excess of which forms conditions for oxidative stress. For a whole host of reasons, the brain is very vulnerable to oxidative stress: its tissues are adapted to intensive O_2 consumption, contain more oxidizable substrates, and have a less active antioxidant defense system. Catalase (H_2O_2-oxidoreductase, 1.11.1.6) is one of the key enzymes of the antioxidant system. Catalase provides transformation of peroxide (H_2O_2), a product of side reactions in the mitochondrial respiratory chain, into water and O_2. A peculiarity of brain tissues is a very low catalase activity in comparison with that of other organs [Galkina, 2013]. The different activity of antioxidant enzymes and the intensity of spreading of thiobarbituric acid (TBA) reaction products in the brain compartments [Mizuno, Ohta, 1986] may be indicative of different degrees of their vulnerability to ROS.

In contrast to mammals, hypoxia-tolerant animals provide an opportunity, under experimental conditions, to activate or block selectively single parts of the whole mechanism of survival in order to assess their functions. A 90-fold increase of extracellular [GABA] leading to a coma-like state is observed under anoxia in the brain of a turtle *Chrysemys picta belli* tolerant to O_2 deficiency [Nilsson et al., 1991]. [GABA] increases only 2-fold in the hypoxic brain of crucian carp, while motion activity is maintained [Hylland, Nilsson, 1999]. It is known that the effect of excitatory and inhibitory neurotransmitters appears only upon the release from intracellular stores. The administration of a GABA mimetic (phenibut, γ-amino-β-phenylbutyric acid hydrochloride) makes it possible to recreate features of the GABAergic link activation and evaluate GABA influence on the oxidoreductase functioning similar to that during acute hypoxia/anoxia.

Teleosts are a convenient experimental neurobiological object that allows the data obtained to be extrapolated to higher vertebrates and humans. A zebrafish *Danio rerio*, the most famous Teleostei representative among model organisms, has a high homology with the human genome (about 70%) in view of a certain physiological similarity of the main organ systems and tissues [Lim et al., 2022].

The Black Sea scorpionfish (ruff) *Scorpaena porcus* Linnaeus, 1758 is a hypoxia-tolerant teleost. The scorpionfish is able to survive under severe hypoxia conditions (0.35 $mg\,O_2{\cdot}L^{-1}$ for 4 h) [Soldatov et al., 2021] and can recover after 20–30 min of asphyxia resulting from air exposure [Lushchak et al., 1998]. Establishing features of the GABA function implementation, which allow such vertebrates, as the scorpionfish, to survive with little O_2 or being deprived of it, offers a new look at the problems associated with hypoxia and possible ways of counteracting hypoxic brain damage.

The objective of this study was to investigate the effect of phenibut on oxidoreductase activity in the brain compartments of adult and juvenile scorpionfish.

MATERIAL AND METHODS

Scorpionfish *S. porcus* used for the present study were captured in July 2023 in the Sevastopol Bay using a seine net and were transferred to a laboratory in aerated 60-L plastic tanks within 2–3 h after capture. After transportation, the fish were placed into a flow-through aquarium for one week. The animals were fed on minced fish flesh, and only robust, actively feeding fish specimens were used for further experiments.

The study was carried out using a specially designed stand that made it possible to stabilize the required temperature and oxygen concentration for an unlimited period. The water temperature in the experimental chamber was maintained at the seawater temperature level in the summer season (+21…+22 °C). All fish were kept at oxygen concentration of 5.6–6.7 $mg\,O_2{\cdot}L^{-1}$ in water (normoxia). The oxygen level in water was monitored potentiometrically with an oxygen sensor ELWRO PRL T N5221 (Poland).

Experiments were carried out on adult ($n = 16$; body length 12–18 cm; weight 70–250 g; gonadal maturity stage IV–V) and juvenile scorpionfish ($n = 16$; body length 8.5–12.0 cm; weight 35–63 g; gonadal maturity stage I) divided into the control and experimental groups (8 specimens in each group). In the experimental groups, a GABA mimetic, phenibut, was injected intraperitoneally (400 $mg{\cdot}kg^{-1}$, i. p.); after that, the animals were returned to the darkened experimental chamber for 60 min. The scorpionfish did not manifest any signs of intoxication or movement disorders after phenibut administration and till the removal of tissue samples.

Fish in the control and experimental groups were killed by transspinal dissection. Brain tissues were sampled on an ice table, (0 ± 4) °C, immediately after fish decapitation and were divided into two parts: medulla oblongata (MB) and forebrain, midbrain, and diencephalon (AB). The weighed brain samples were instantly frozen on dry ice and stored at −80 °C until analysis (Forma 900 Series, Thermo Scientific, USA). The supernatant was obtained by centrifuging the homogenates in an Eppendorf 5424 F centrifuge (refrigerated) at 10,000 rpm for 15 min.

The activities of cytoplasmic oxidoreductases, malate dehydrogenase and lactate dehydrogenase (MDH and LDH, respectively), were evaluated using spectrophotometric measurements of the speed of NADH oxidation in 0.2 M Tris-HCl buffer (pH 7.5) in a 3-mL quartz cuvette with 10-mm pathlength at a wavelength $\lambda = 340$ nm and +25 °C. The reaction was initiated by adding

0.025–0.05 mL of extract, and the measurements were taken every 30 s during 2–3 min. Pyruvate was used as a substrate to measure LDH activity, and oxaloacetate was used to measure MDH activity. Each measurement was repeated 2–3 times, and the values of the corresponding measurements were averaged. Specific activity of oxidoreductases was expressed as μmol NADH$\cdot$min$^{-1}\cdot$mg^{-1} of supernatant protein. The ratio of the cytosolic MDH/LDH was defined as MDH activity divided by LDH activity, and this allowed evaluating a potential capacity to conduct aerobic metabolism.

Catalase activity (H_2O_2: H_2O_2-oxidoreductase; 1.11.1.6) was assessed by the change in extinction at $\lambda = 410$ nm by a method based on the ability of hydrogen peroxide to form a colored complex with ammonium molybdate. The measurements were repeated two times, and the results were averaged. The tubes were filled with 1 mL of 0.03% hydrogen peroxide solution, 0.25 mL of 0.05 M phosphate buffer, pH 8.0, and 0.05 mL of supernatant. The control sample contained 0.25 mL of 12 mM sodium azide solution. After samples incubation for 10 min at +25 °C, the reaction was stopped by adding 2 mL of 4% ammonium molybdate solution. The specific activity of catalase was expressed in μM $H_2O_2\cdot$min$^{-1}\cdot$mg^{-1} of supernatant protein.

Protein content was estimated using the micro-biuret method. The colorimetric reaction was carried out at +25 °C for 15 min, and the optical density was measured at $\lambda = 330$ nm. Crystalline serum albumin was used as a standard for creating a calibration curve.

The MDH/catalase and LDH/catalase indices were calculated based on the oxidoreductase activity, in relation to which the ratio of the intensity of functioning of energy metabolism pathways to metabolic tension was assessed.

Data are presented as mean ± *SD*. The normality of data distribution was checked by the Pearson's test. Statistical comparisons were made using the two-sided Student's *t*-test. The differences were considered statistically significant at $p < 0.05$. The two-sided correlation coefficient (r) between MDH, LDH, and catalase activity in the brain compartments was calculated applying the Spearman's rank correlation coefficient. Statistical analysis and graphic representation of the obtained data were carried out using the standard software package of MS Office Excel.

RESULTS

Oxidoreductase activity in the brain compartments of adult and juvenile scorpionfish. In MB and AB of adult scorpionfish, MDH activity was almost identical, while in AB of juvenile individuals, this index was slightly increased (Fig. 1a). In its turn, LDH activity in the brain samples of adult and juvenile fish was lower than that of MDH (Fig. 1b).

Similar rates of catalase activity for the brain compartments in adult individuals contrasted with the lower activity of this enzyme in juvenile fish (Fig. 1d). The lowest catalase activity was registered in juvenile AB ($p < 0.05$).

A trend towards higher values of MDH/LDH index in the mature brain of scorpionfish was observed (Fig. 1d). The lowest ratio of MDH/LDH was recorded in MB of juveniles ($p < 0.05$) (Fig. 1d). At the same time, the values of MDH/catalase and LDH/catalase indices in the brain regions of juveniles exceeded those in adults ($p < 0.05$) (Fig. 2).

MDH and LDH activities in MB of adult scorpionfish positively correlated with body weight ($r = 0.65$ and $r = 0.80$, respectively; $p < 0.05$) and body length ($r = 0.67$ and $r = 0.80$, respectively; $p < 0.05$). Alongside with that, a close relationship was established between MDH and LDH activity in their AB and body weight ($r = 0.62$ and $r = 0.60$, respectively; $p < 0.05$), as well as that of LDH activity and body length ($r = 0.66$; $p < 0.05$).

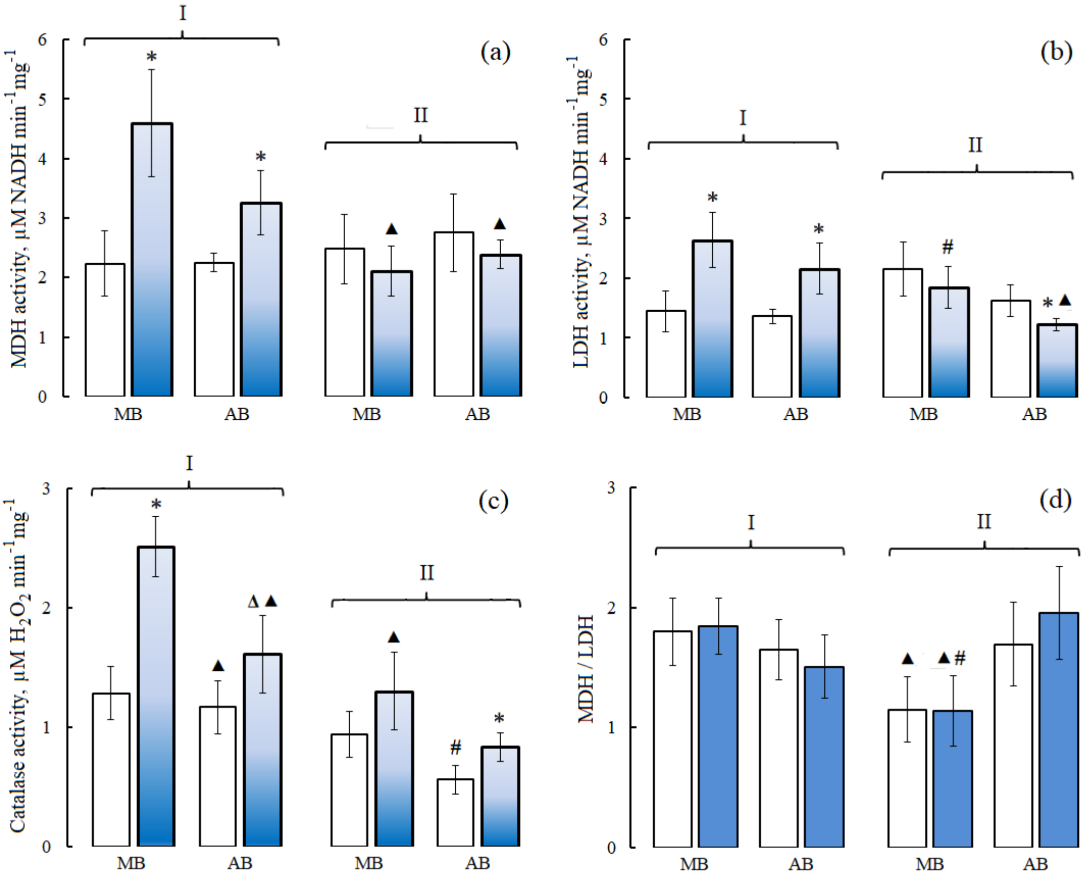

Fig. 1. Effect of phenibut on the activity of MDH (a), LDH (b), and catalase (c) and MDH/LDH index (d) in the brain compartments of *Scorpaena porcus*. White bars, control; dark bars, experiment. I, adults; II, juveniles. MB, medulla oblongata; AB, anterior brain compartments. Significant difference, $p < 0.05$: *, *vs.* control; ▲, *vs.* the same brain compartment of another age group; Δ, between brain compartments of adults; #, between brain compartments of juveniles

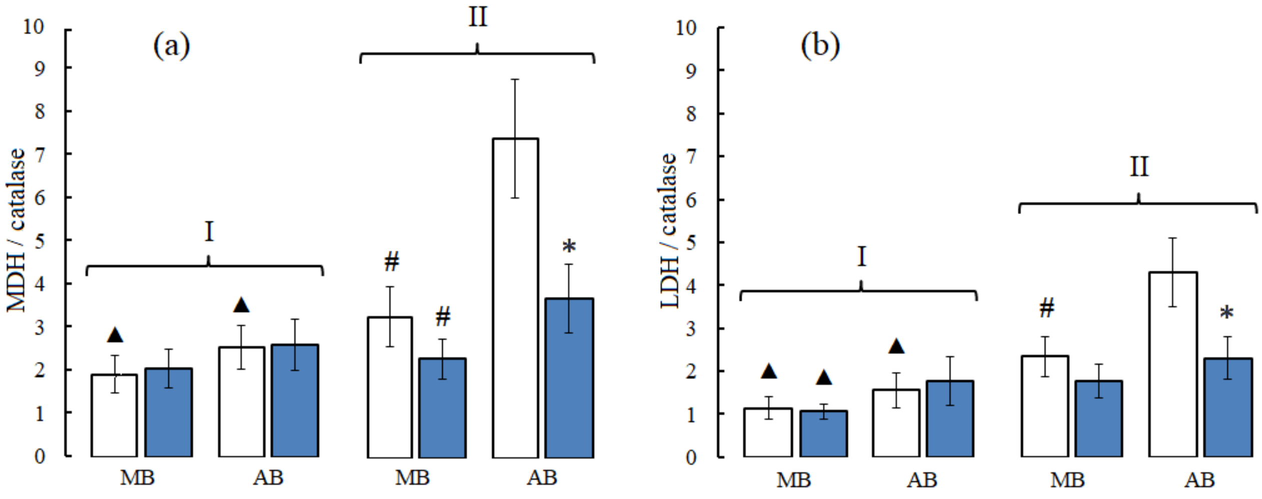

Fig. 2. Effect of phenibut on the ratio of oxidoreductase activity in the brain compartments of *Scorpaena porcus*. White bars, control; dark bars, experiment. A, MDH/catalase; b, LDH/catalase. I, adults; II, juveniles. MB, medulla oblongata; AB, anterior brain compartments. Significant difference, $p < 0.05$: *, *vs.* control; ▲, *vs.* the same brain compartment of another age group; #, between brain compartments of juveniles

Oxidoreductase activity in the brain compartments of adult and juvenile scorpionfish under the effect of phenibut. After phenibut administration, MDH activity increased significantly – 2.1-fold and 1.5-fold in MB and AB of adult individuals, respectively ($p < 0.05$) – reaching 4.60 μM NADH·min^{-1}·mg^{-1} of protein in MB and 3.26 μM NADH·min^{-1}·mg^{-1} of protein in AB (Fig. 1a). At the same time, LDH activity rose 1.8-fold in MB and 1.6-fold in AB ($p < 0.05$) acquiring a maximum value in MB: 2.64 μM NADH·min^{-1}·mg^{-1} of protein.

After phenibut administration to juveniles, MDH and LDH activity in their brain compartments decreased insignificantly, with the exception of AB (Fig. 1a), where LDH activity decreased from 1.63 to 1.22 μM NADH·min^{-1}·mg^{-1} of protein ($p < 0.05$). Compared to the adult group, in juvenile fish, MDH activity was lower in MB and AB, and LDH activity was lower in AB ($p < 0.05$). Differences between the brain regions of juveniles were established only in LDH activity under experimental conditions ($p < 0.05$).

It should be noted that after phenibut administration, LDH activity in the fish brain structures remained significantly lower than MDH activity ($p < 0.05$).

At the same time, catalase activity increased in all brain compartments of scorpionfish in both age groups treated with phenibut ($p < 0.05$) (Fig. 1c). The most prominent shifts were observed in MB of mature scorpionfish: the enzyme activity was almost doubled ($p < 0.05$) and amounted to 2.51 μM H_2O_2·min^{-1}·mg^{-1} of protein. Catalase activity increased from 0.54 to 0.83 μM H_2O_2·min^{-1}·mg^{-1} of protein in AB of juveniles (Fig. 1b). At the same time, catalase activity in immature fish remained significantly lower compared to that of adults ($p < 0.05$).

A close relationship was found between MDH and LDH activities in MB ($r = 0.93$; $p < 0.05$) and AB ($r = 0.91$; $p < 0.05$) in juveniles, as well as in adult fish (Table 1).

Table 1. Correlation coefficient (r) between MDH and LDH activities in the brain compartments of adult and juvenile *Scorpaena porcus* after phenibut administration

Tissues	Adults		Juveniles	
	Control	Phenibut	Control	Phenibut
Medulla oblongata	0.92**	0.63*	0.93**	0.77*
Anterior brain compartments	0.92**	0.80*	0.91**	0.60*

Note: *, $p < 0.05$; **, $p < 0.01$.

Примечание: * — $p < 0{,}05$; ** — $p < 0{,}01$.

MDH/LDH ratio in the brain of adult scorpionfish did not change significantly under the effect of phenibut (Fig. 1d), and a weak trend towards its decrease was observed only in AB. MDH/catalase and LDH/catalase indices also showed some stability (Fig. 2). Alongside with that, a decline of the above-mentioned indices was registered practically in all brain compartments of immature scorpionfish (Fig. 2).

Previously noted high values of the correlation coefficient between MDH and LDH activity in the brain compartments of different age groups of scorpionfish slightly decreased under the effect of phenibut (Table 1). Moreover, phenibut administration canceled the initially established correlation dependence of oxidoreductase activity on the weight and length of adult fish.

DISCUSSION

Age-related features of MDH and LDH activity in the brain compartments of scorpionfish. The brain regions of adult and juvenile scorpionfish were characterized by comparable values of MDH activity, although this parameter was slightly higher in juveniles.

A weak trend to an increase in MDH activity in the brain of juveniles (especially in AB) may serve as an age-related feature of the maturing brain that consumes energy on plastic processes, synaptogenesis, and myelination. In particular, brain development in rats, reaching sexual maturity by two months of age, is completely terminated only on the 90th day after birth, when myelination is completed in the cerebral cortex [Bon, 2021]. Alongside with that, the intensity of energy metabolism in the brain can be indirectly related to the lifestyle and nutrition. Juvenile scorpionfish live mainly on small crustaceans, molluscs, and worms hiding in the thickets of aquatic plants, while adult individuals prefer fish. AB structures can be relatively more active in juveniles compared to adult ambush predators due to differences in foraging behavior. In addition, AB includes the centers of regulation of muscle tone and body balance coordination, as well as smell and vision centers that are necessary for defensive behavior, since juvenile fish are a relatively easy prey for large predators.

LDH activity in the brain of juvenile scorpionfish noticeably exceeded that of adult fish. As shown, the LDH activity level in the fish brain is a significant part of the mechanism of resistance to hypoxia making it possible to endure O_2 starvation and adapt to low PO_2 [Mandic et al., 2013]. Obviously, increased LDH activity in the brain of juvenile scorpionfish (MB and AB) is a part of an adaptive apparatus that enhances the survivorship of young individuals under conditions of varying O_2 in aquatic environments.

There is a close correlation between MDH and LDH activities in the brain compartments of scorpionfish which reflects the features of the regulation of metabolic pathways during energy production. The mixed aerobic and anaerobic functions of MDH occupying an intermediate position between glycolytic enzymes and citrate synthase should be taken into account. Moreover, the activity of abovementioned oxidoreductases in both brain compartments of adult fish and in MB of immature individuals was positively correlated with body weight. At the same time, an identical positive relationship between oxidoreductase activity and body length was observed in adult fish, and it was completely absent in immature scorpionfish. The changes in energy metabolism during growth have been reported in many fish species and may reflect the way organisms deal with environmental constraints [Almeida-Val et al., 2000]. Such a positive correlation of MDH and LDH with the body size of juvenile *Astronotus ocellatus* allows them to increase their anaerobic potential with growth [Almeida-Val et al., 2000]. It is obvious that survivorship under hypoxia will rise due to a combination of effects of metabolic rate suppression and an increase in anaerobic capacity as the fish grow. At the same time, the constancy of LDH and pyruvate kinase activity in the brain tissues of adult individuals of bathybenthic species (the barred sand bass *Paralabrax nebulifer* and kelp bass *Paralabrax clathratus*) was observed over a wide range of body sizes [Somero, Childress, 1980] which probably reflects the reaching of a certain plateau in the adaptive capability of the mature brain.

Thus, apparently, the degree of MDH and LDH activity in the brain structures in different age groups of scorpionfish is closely intertwined with the lifestyle, including foraging and defensive behavior and the features of biochemical mechanisms of adaptation.

Age-related features of MDH and LDH activity in the brain compartments of scorpionfish under the effect of phenibut. During hypoxia, the amount of released GABA is determined by species differences and the brain's need for metabolic depression which, in turn, depends on the ability for anaerobic ATP production. The extracellular level of neurotransmitters is approximately 1/1000 of intracellular stores in the brain cells. The administration of GABA or its agonists makes it possible to reconstruct the "manners" of metabolic pathways under acute hypoxia *in vivo*. Since hypoxic GABA release is subjected to significant individual variations [Hylland, Nilsson, 1999], the injection of a GABA mimetic when converted to the body weight of model organisms allows to standardize and detail the influence of GABA on the mechanisms providing the tolerance to O_2 starvation. One of such agents, phenibut, is a nonselective GABA agonist and GABA mimetic affecting both ionotropic GABA(A) and metabotropic GABA(B) receptors.

In the brain compartments of adult scorpionfish, phenibut administration led to a simultaneous increase in MDH and LDH activity, with an opposite trend towards a notable decrease in LDH activity, *i. e.*, limitation of anaerobic glycolysis in the juvenile brain.

The importance of cytoplasmic MDH rises, when there is a need to enhance glycolytic capacity. MDH may support glycolysis in the absence of O_2, since it delivers NAD^+ as a key cofactor required for functioning of glyceraldehyde-3-phosphate dehydrogenase (GAPDH). In its turn, the function of GAPDH as a catalyst is meant to accelerate the reversible oxidative phosphorylation of glyceraldehyde-3-phosphate to 1,3-diphosphoglycerate with NADH formation. During cerebral ischemia, a simultaneous increase in the activity of mitochondrial and cytosolic MDH forms accompanied by an increase in malate is associated with the activation of the malate-aspartate shuttle mechanism for transporting reduced equivalents from cytoplasm into mitochondria [Belenichev et al., 2012].

Simultaneously with an increase in MDH activity, LDH activity under the effect of phenibut also enhanced in the brain of adult scorpionfish. During hypoxia, such a rise in LDH activity fulfils the immediate energy demand for overcoming possible consequences of insufficient O_2 intake. In particular, such an increase in LDH activity during hypoxia is observed in muscles of a catfish *Clarias batrachus* tolerant to O_2 deficiency [Tripathi et al., 2013]. As a dietary supplement, GABA also caused a gain in LDH activity in liver tissues of a hypoxia-tolerant Indian major carp, mrigal *Cirrhinus mrigala*, during O_2 starvation [Varghese et al., 2020]. At the same time, LDH activity in mrigals under the effect of GABA was somewhat lower than that when exposed to hypoxia. The term “pseudohypoxia” is often used to indicate the activation of the pathway to a decrease in O_2 availability under non-hypoxic conditions. Obviously, an increase in LDH activity in the brain compartments of adult scorpionfish subjected to phenibut administration and in the presence of a sufficient amount of O_2 may correspond to the above notion, *i. e.*, it gives evidence of the reaction of this enzyme according to the “pseudohypoxic” type.

The simultaneous increase in MDH and LDH activity against the backdrop of phenibut reflects an enhanced intensity of glycolytic processes in scorpionfish. The occurring discrepancy in the degree of shifts in the oxidoreductase activity in different brain structures may be a consequence of significant differences in the rate of GABA metabolism and specificity of GABA effect on energy metabolism in the separate brain regions.

Noteworthy, phenibut administration contributed to a decrease in LDH activity (especially in AB) in the absence of a noticeable MDH reaction in juvenile scorpionfish *vs.* mature individuals. It is possible to explain LDH “behavior” in the age-related aspect only using a number of certain assumptions.

Hence, a decrease in LDH activity in juvenile scorpionfish (during catalase activation associated with a probable increase in H_2O_2 production) can be conditioned by oxidation of cysteine residues by ROS in the enzyme molecule determining the formation of its spatial configuration [Ledo et al., 2022].

In addition, variations in the response of oxidoreductases to phenibut in scorpionfish individuals of different age may be indirectly related to the phenomenon of transit of GABA mediator function. It is known that GABA excitatory action is observed in higher vertebrates only at the early stages of development (embryogenesis and early postnatal period) [Ben-Ari, 2014]. In the perinatal period, GABA effect shifts from excitation to inhibition and, accordingly, from depolarization to hyperpolarization of the cell membrane [Ben-Ari, 2014]. Transit of GABA function is mediated through the developmentally regulated expression of cation-Cl-cotransporters NKCC1 (Na^+-K^+-Cl^- cotransporter 1) and KCC2 (K^+-Cl^- cotransporter 2). It is assumed that the ratio between NKCC1 and KCC2 activities providing incoming and outgoing Cl^- fluxes, respectively, plays a key role in functioning of GABA(A) receptors [Virtanen et al., 2021]. A decrease in NKCC1 activity with an increase in KCC2 activity is the cause for a sharp change in the properties of GABA(A) receptors during mammalian ontogenesis.

After the final formation of interneuronal connections and the establishment of constant network activity, time-averaged Cl^- loading, KCC2 expression level, and hyperpolarizing effect of GABAergic currents reach their peak values [Virtanen et al., 2021]. Alongside with that, ion transport and energy metabolism of neurons tend to their maximum values. In its turn, the neuronal damage leads to KCC2 loss and to a "reversal" of the polarity of GABAergic currents which may be a part of a larger pattern of dedifferentiation that is necessary for the neuronal survival in adverse conditions [Virtanen et al., 2021] and is manifested by a return to immature high [Cl^-] and the excitatory effect of GABA [Ben-Ari, 2014].

The excitatory/inhibitory sequence of GABA function is just one of many aspects of the maturation of brain activity. Since the shift from one to a diametrically opposite functional role of GABA occurs in higher vertebrates at the prenatal and postnatal developmental stages, the oxidoreductase reaction is likely to be observed in the brain of juvenile scorpionfish against the backdrop of a slowed transit of the mediator function (transitional stage of the GABA function) to the classical inhibition of neuronal activity. In case of a possible prolonged transit of the GABA function, the difference and direction of the change in LDH activity in MB and AB of juveniles *vs.* mature scorpionfish correlates directly with the unfolding of KCC expression in the caudal-to-rostral direction in the process of brain maturation [Watanabe, Fukuda, 2015]. At the same time, phenibut makes it possible to maintain the interdependence (observed in the control) between MDH and LDH activity in different brain compartments of juvenile and adult scorpionfish which is indicative of a rather physiological, but not toxic effect of this agent.

Age-related features of catalase activity in the brain compartments of scorpionfish. Energy metabolism is both a source and a target for various oxidants which determines the close coordination of enzymes of metabolic pathways and the antioxidant system. Brain tissue is notable for a particular intensity of oxidative phosphorylation (hereinafter OXPHOS) which makes this tissue more susceptible to oxidative stress. The main source of ROS is the leakage of electrons from the mitochondrial electron transport chain. Approximately 2–5% of the electron flow in the respiratory chain of isolated brain mitochondria produce superoxide anion (O_2^-) and H_2O_2. The high dependence of the brain on ATP production *via* intensive OXPHOS determines the necessity for effective methods of O_2^- and H_2O_2 detoxification. O_2^- is inactivated by superoxide dismutase (SOD). H_2O_2 formed in this process is decomposed by catalase and glutathione peroxidase (hereinafter GPx). While catalase serves as the main H_2O_2 detoxification enzyme, GPx is more efficient in H_2O_2 decomposition [Bagnyukova et al., 2005]. Moreover, GPx has a much higher affinity for H_2O_2 which suggests the importance of GPx at low H_2O_2 concentrations, while the role of catalase increases under severe oxidative stress.

The brain antioxidant system is characterized by a low or moderate activity of catalase and GPx against the backdrop of the predominant SOD activity [Bagnyukova et al., 2005]. The low catalase activity may be associated with the production of H_2O_2 as a transmitter which acquires a specificity in mediating signaling effects [Sies, Jones, 2020] and has the ability to modulate synaptic transmission [Lee et al., 2015]. The level of antioxidant enzyme activity in fish has features that are characteristic and inherent to certain species, and this makes it difficult to compare the antioxidant system parameters [Radi et al., 1985]. Moreover, the discrepancies in the activity of antioxidant enzymes in relation to the brain structures manifest morphological and functional heterogeneity of the brain [Brannan et al., 1981].

Catalase activity in MB was slightly higher than that in AB in both age groups of scorpionfish. The brainstem neurons in the mammalian brain (including MB) have a relatively high degree of catalase immunoreactivity compared to those of the forebrain [Moreno et al., 1995]. However, within the brain structures themselves, there are regions with different catalase staining intensity [Moreno et al., 1995]. In many cases, densely stained cells appear to be more resistant to ischemia/reperfusion injury, whereas weakly stained cells are more susceptible to ischemic injury.

The manifestation of catalase activity in the brain compartments of scorpionfish can be regarded in two ways. On the one hand, high activity of antioxidant enzymes (catalase in particular) may be of certain importance for scorpionfish MB that contains cardiorespiratory reflexogenic centers and ensures its viability. On the other hand, AB in a resting ambush predator should be less active functionally at the appropriate OXPHOS intensity and at a lower rate of ROS/H_2O_2 production.

H_2O_2 is considered a dynamic reporter of neuronal activity and a "translational substance" blurring the boundary between energy and information [Lee et al., 2015]. O_2 consumption is believed to be proportional to the activity of brain structures which are characterized by the greatest demand for macroergs in order to support ATP-dependent signaling, *i. e.*, information processes. H_2O_2 produced during OXPHOS rapidly retranslates dynamic shifts in cellular metabolism, especially in the mitochondrial O_2 consumption, into a meaningful physiological signal [Lee et al., 2015]. H_2O_2-sensitive ion channels are the target of such a physiological signal and can affect the excitability of neurons directly producing H_2O_2. H_2O_2 can modulate GABAergic neurotransmission. Cellular transient receptor potential (TRP) ion channels, subclass TRPM2 (transient receptor potential melastatin 2, non-selective cation channel), are uniquely sensitive to the action of H_2O_2, and this leads to the activation of GABAergic neurons. At the same time, such activation of KATP channels (ATP-dependent potassium channels) by H_2O_2 reduces neuronal excitability [Lee et al., 2015]. There are certain differences in the H_2O_2-dependent activation of KATP and TRPM2 channels for different animal species which is indicative of special functions of this regulatory process. Apparently, the resulting effect of H_2O_2 will reflect the balance of activity of the expressed H_2O_2-sensitive target channels (KATP and TRPM2) and thus ensure cellular type-specific modulation patterns.

It should be noted that catalase activity in different brain compartments of juvenile scorpionfish (especially AB) was lower compared to that of adult individuals, and this is consistent with the data on a gain in catalase activity in the mammalian brain in the process of its maturation from the postnatal period to full maturity [Mavelli et al., 1982] and on a further age-dependent increase in the enzyme activity [Vertechy et al., 1993]. On the other hand, under normal conditions, low catalase activity is partially compensated by GPx function [Bagnyukova et al., 2005]. In addition, total glutathione level is quite high in the brain of goldfish highly tolerant to hypoxia (670 nmol *per* g wet weight) which indicates the importance of this antioxidant tripeptide in H_2O_2 neutralization. In its turn, low GPx activity can be compensated by high catalase activity. The activity of the mentioned enzymes is negatively correlated in different mammalian species [Godin, Garnett, 1992]. Thus, GPx is likely to maintain cellular function and adapt to the normal cellular metabolic activity, while catalase will be a part of the stress response mechanism regardless of low metabolic rate or O_2 concentration in the aquatic environment. Moreover, catalase does not require cofactors or energy expenditure for its activity, while GPx oxidizes glutathione to GSSG that must then be processed by NADPH-dependent glutathione reductase. The preference for an enzyme with minimal energy consumption in the environment with limited availability of resources may be an effective survival strategy, especially for immature animals.

Relatively low catalase activity may suggest an increase in H_2O_2 level in the brain regions of juvenile scorpionfish. As mentioned above, H_2O_2 is assigned the function of a volume neurotransmitter [Ledo et al., 2022] and of a second messenger as well [González et al., 2020]. O_2-dependent production of H_2O_2 is a regulator of the erythropoietin (Epo) gene expression [Fandrey et al., 1994], a "multi-purpose" factor of general oxygen homeostasis. In particular, Epo exerts protective functions in different organs, including brain, in case of ischemic injury [Grasso et al., 2004]. Epo gene and Epo receptor (EpoR) expression has been identified in teleost species [Chu et al., 2007].

A decrease in catalase activity is likely to ensure functioning of H_2O_2 as a second messenger in juvenile scorpionfish which provides their adaptive potential and survivorship in hypoxia.

As mentioned above, calculated MDH/catalase and LDH/catalase indices reflect the ratio of energy metabolism intensity to physiological tension (eustress). Adult scorpionfish, as well as juvenile ones, were similarly characterized by slightly higher MDH/catalase and LDH/catalase indices in AB. Moreover, MDH/catalase and LDH/catalase in juvenile individuals were noticeably higher ("their own" age norm), since less intense functioning of "energy-saving" catalase may be associated with an increased "need" for H_2O_2 as a second messenger in the processes of brain maturation and adaptation. Aerobic and anaerobic pathways of energy metabolism in the brain of juvenile scorpionfish that supply ATP for the protein synthesis, the development, and maintenance of synaptic transmission of neural networks acquire special significance. At the same time, a sufficient amount of H_2O_2 ensures the transcription of genetic factors.

Age-related features of catalase activity in the brain compartments of scorpionfish under the effect of phenibut. Increased catalase activity under the effect of phenibut in the scorpionfish brain may serve as an indirect sign of large-scale H_2O_2 production. Any stress response of the organism is accompanied by a short-term burst in ROS production and the development of oxidative stress. A putative increase in H_2O_2 production in the scorpionfish brain under phenibut administration is associated with the ability of GABA derivatives to stimulate OXPHOS [Mokrousov et al., 2019]. In MB of adult scorpionfish, catalase activity reached the highest value among the studied brain samples which may indirectly evidence for the dominant functional activity of this part of the brain of the ambush predator, as mentioned above.

For successful survival in hypoxia, an organism must not only maintain its viability amidst O_2 shortage, but also have an effective mechanism to minimize or prevent oxidative stress during the transition from hypoxia back to aerobic conditions. Some animal species consistently demonstrate high levels of the activity of antioxidant system, while the others increase the antioxidant defense directly on exposure to hypoxia in an anticipatory process coined "preparation for oxidative stress" [Hermes-Lima et al., 1998]. The latter mechanism occurs in stress-tolerant species that are regularly exposed to significant fluctuations in O_2 availability in their habitat [Víg, Nemcsók, 1989]. The enhancement of antioxidant defense during physiological states requiring decreased ROS production is a preparative mechanism that minimizes potential damage due to oxidative stress, including reoxygenation. It is obvious that phenibut has the properties of an agent quickly increasing the antioxidant status of the scorpionfish brain.

The ability of exogenous GABA to enhance H_2O_2 production [Jin et al., 2019] which provides modulation of the currents mediated by GABA(A) receptors constitutes a reversible redox-sensitive signaling mechanism [Hogg et al., 2015]. H_2O_2 can limit GABAergic neurotransmission not only through the effect on presynaptic sites [Sah, Schwartz-Bloom, 1999], but also on postsynaptic sites [Sah et al., 2002]. ROS-induced plasticity of different GABA(A) receptor subtypes suggests oxidation of cysteine residues by ROS in receptor subunits, and this is critical for ion channel activation [González et al., 2020]. In addition, it was shown that the activation of a special type of GABA(A) receptors by ROS, including $\alpha3$ subunit, may enhance GABAergic synaptic transmission [Accardi et al., 2014]. Obviously, ROS, as a putative homeostatic signaling unit, couple the cellular metabolism with the "strength" of inhibitory neurotransmission [Accardi et al., 2014].

Anyway, the effect of ROS on GABAergic signaling and the resulting effect is likely to depend entirely on the cell type and the region of the central nervous system [González et al., 2020]. The sensitivity of GABA(A) receptors to ROS/H_2O_2 remains an important factor in the development of neuronal injury during ischemia and neurodegenerative processes [Accardi et al., 2014].

The MDH/catalase and LDH/catalase indices, before and after phenibut administration in the different brain compartments of adult scorpionfish, remained comparable which is indicative of the stability of functioning of energy metabolism pathways without signs of oxidative stress. At the same time, a sharp reduction in similar indices, especially in AB, was observed in juvenile scorpionfish which was determined by a decrease in the activity of energy metabolism-related oxidoreductases and by the increased catalase activity. As MDH/LDG index in MB of adult and juvenile scorpionfish turned out to be quite stable, it is possible to assume greater stability and protection of this part of the brain. However, a simultaneous decrease in MDH/catalase and LDH/catalase in the brain compartments of juveniles indicates pronounced physiological tension. A decline in the mentioned ratios of oxidoreductase/catalase activity occurred mainly due to catalase activation which can be regarded as an indirect sign of a rise in the production of substrate (H_2O_2) for this enzyme. Given that H_2O_2 actually acts as a second messenger [González et al., 2020], the physiological meaning of increased H_2O_2 production is to trigger a regulatory cascade providing increased antioxidant protection through ROS-sensitive transcription factors [Bagnyukova et al., 2005] as a protective mechanism in the maturing brain.

Conclusions. The brain of juvenile scorpionfish is characterized by a trend toward a higher intensity of energy metabolism which may be determined by the completion of growth processes, with a noticeably lower catalase activity. In the mature fish brain, GABA mimetic phenibut causes activation of oxidoreductases according to a "pseudohypoxic" scenario. At the same time, activation of the GABAergic mechanism can suppress LDH activity in the anterior brain compartments of juvenile fish that are more vulnerable to O_2 starvation. A concomitant increase in catalase activity in the brain tissues of both age groups is probably indirect evidence of an increase in H_2O_2 production due to OXPHOS intensification. Deviations in catalase activity are likely to contribute to the implementation of the function of H_2O_2 as a second messenger and a modulator of GABAergic signaling. Such a mechanism involving H_2O_2 may be especially significant for the maturing brain that completes the adjustment of neural networks and also ensures and maintains brain resistance to hypoxia in juvenile and adult scorpionfish.

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ВЛИЯНИЕ МИМЕТИКА ГАМК ФЕНИБУТА НА АКТИВНОСТЬ ОКСИДОРЕДУКТАЗ В КОМПАРТМЕНТАХ МОЗГА ВЗРОСЛЫХ И НЕПОЛОВОЗРЕЛЫХ ОСОБЕЙ СКОРПЕНЫ *SCORPAENA PORCUS* LINNAEUS, 1758

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Повышение уровня ГАМК служит выживанию нейронов при гипоксии/аноксии. В процессе онтогенеза ГАМК способна трансформировать свою медиаторную функцию от возбуждающей к тормозной. Изучали активность оксидоредуктаз (МДГ, 1.1.1.37; ЛДГ, 1.1.1.27; каталазы, 1.11.1.6) в отделах мозга — продолговатом мозге (МВ) и переднем, промежуточном и среднем мозге (АВ) — неполовозрелых и взрослых особей морского ерша *Scorpaena porcus* на фоне введения миметика ГАМК фенибута (400 мг·кг$^{-1}$, i. p.). Структуры АВ неполовозрелых особей скорпены характеризовались интенсивностью аэробного метаболизма, сопоставимой с таковой взрослых особей; в то же время в МВ и АВ молоди была отмечена более высокая активность ЛДГ, служащая, по-видимому, повышению выживаемости при низком PO_2. В обеих возрастных группах показатели активности каталазы были несколько выше в МВ, что может быть связано как с интенсивностью окислительного фосфорилирования, так и с устойчивостью к повреждению МВ при гипоксии. При этом активность каталазы в мозге молоди (особенно АВ) была несколько ниже показателей взрослых особей. Фенибут повышал активность МДГ и ЛДГ в компартментах мозга взрослых особей скорпены, что, вероятно, связано с активацией малат-аспартатного шунта, при противоположном тренде к ограничению анаэробного гликолиза в незрелом мозге, особо выраженном в АВ ($p < 0,05$). Одновременно фенибут способствовал увеличению активности каталазы во всех компартментах мозга вне зависимости от возраста скорпены ($p < 0,05$); наибольшей величины активность каталазы достигала в МВ взрослых особей ($p < 0,05$). Предполагается, что контролируемая каталазой продукция H_2O_2 переводит изменения в клеточном метаболизме в значимый физиологический ответ путём воздействия на H_2O_2-чувствительные ионные каналы, которые определяют возбудимость нейронов, и модулирует ГАМКергическую передачу сигналов. Такой механизм может быть задействован при созревании мозга, поддерживать устойчивость мозга к гипоксии и обеспечивать адаптационные процессы неполовозрелых и взрослых особей скорпены.

Ключевые слова: костистые рыбы, мозг, фенибут, ГАМК-рецепторы, оксидоредуктазы

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A GASTROPOD *PATELLA ULYSSIPONENSIS* GMELIN, 1791 (GASTROPODA: PATELLIDAE) FROM THE CAUCASIAN BLACK SEA SHELF: BIOLOGICAL INVASION OR RECOVERY OF THE NATIVE POPULATION?

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In spring 2023, an abundant population of adult gastropods *Patella ulyssiponensis* Gmelin, 1791 was recorded in the Sochi port area. *P. ulyssiponensis*, also known as a limpet, is an inhabitant of contour biotopes and a crawling edible gastropod. This species is listed in Red Data Books of the Black Sea, the Crimea, and Sevastopol and still does not occur on shelves of the Crimea, Ukraine, Romania, Bulgaria, and Turkey. It was not registered on the Caucasian shelf since the middle of the XX century. The paper provides data on distribution, morphological structure, and settlement density of *P. ulyssiponensis* sampled in the Sochi port area in June 2023. According to the severity of radial ribs and their association into bundles, the position of the crown, the morphometry of the shell itself, the color of the shell inner surface, and the integrity or serration of the peristome, the found species was assigned to *P. ulyssiponensis*. In the Black Sea, the limpet is known as *Patella tarentina* Salis Marschlins, 1793, *P. caerulea* var. *tenuistriata* Weinkauff, 1880, and *P. pontica* Milaschewitsch, 1914 (syn.). In earlier works on the Black Sea, it was combined with *P. caerulea* Linnaeus, 1758 endemic to the Mediterranean Sea. *P. ulyssiponensis* abundance reached 240–320 ind.$\cdot$m^{-2} and was higher at the station on the outer side of the southern pier than in the beach area. The limpets we registered were somewhat smaller than those previously noted for the Black Sea. The maximum length of the shell for molluscs of the Sochi port area reached 43.0 mm; width, 17.3 mm; and height, 20 mm. However, these individuals had a higher shell than those of the Black Sea population and the population from the northern Aegean Sea; this is typical for inhabitants of the water's edge. The ratios of the shell height to its length were (0.43 ± 0.05) and (0.45 ± 0.07) for the first and second study areas, respectively. *P. ulyssiponensis* reinvasion to the northeastern Caucasian shelf could be governed by anthropogenic transfer by ships and by natural dispersal. Along with other aspects revealed in recent years in the Black Sea ecosystem, this finding illustrates positive changes in gastropod fauna from the Caucasian shelf.

Keywords: *Patella ulyssiponensis*, distribution, morphometry, density, Sochi port

Since the late 1990s, rare species of zooplankton and zoobenthos more and more often occur in various areas of the Black Sea: the ones that had disappeared during severe pollution, eutrophication of the basin, and pressure by an invasive predator – the warty comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865. The tendency toward ecosystem recovery on the Crimean and Caucasian shelves during the early XXI century coincided with a similar trend observed along the northwestern coast of Ukraine, Romania, and Bulgaria, as well as on the Black Sea coast of Turkey [Arashkevich et al., 2015; Aydın et al., 2021; Filimon, 2020; Kucheruk et al., 2002; Revkov, Boltacheva, 2022; Revkov et al., 2019; Selifonova, 2012; Todorova et al., 2022; *etc.*]. This phenomenon is associated with a shift of the Black Sea ecosystem from a eutrophication phase to a de-eutrophication phase and with a gradual recovery of pelagic and benthic communities [Oguz et al., 2008; Yunev et al., 2007; Zaika, 2011]. Since the 2000s, an increase in abundance of certain populations of previously rare, endangered native species is recorded, and it is accompanied by a mass introduction of invasive, alien species brought in *via* ballast water of merchant ships [Alexandrov, 2004; Çinar et al., 2021; Seebens et al., 2019; Selifonova, 2018; Selifonova et al., 2021; Shiganova et al., 2012; *etc.*].

One of the Black Sea species that disappeared or experienced a drastic population decline during the ecological crisis of the ecosystem is a gastropod *Patella ulyssiponensis* Gmelin, 1791, also known as a limpet. Its absence in published data and in a mollusc collection of the Sochi Geographical Society assembled in the 1960s seems to evidence for the fact that *P. ulyssiponensis* vanished from the Caucasian shelf of the Black Sea in the middle of the XX century. This species was considered critically endangered and was listed in Red Data Books of the Black Sea, the Crimea, and Sevastopol [Black Sea Red Data Book, 1999; Revkov, 2011, 2015]. According to data available, this mollusc still does not occur on shelves of Ukraine, Romania, Bulgaria, and Turkey. The last time *P. ulyssiponensis* was recorded in the Crimea in 2007; however, it is not listed in the Red Data Book of Krasnodar Territory [2017]. Since 2012–2014, researchers from the Sochi Geographical Society, L. Sonicheva and I. Antonova, periodically found single *Patella* spp. along the coast from Lazarevskoye to Adler [Reneva, 2024]. In 2019–2020, the authors observed the mollusc developing in significant numbers not only in Sochi vicinity, but also in Abkhazia, along Pitsunda and Gudauta coasts. In 2017, the online report documented *Patella* spp. finding off the Georgian coast, south of Batumi [Kurakin, 2023]. Observed molluscs were initially identified by the author as *Patella tarentina* Salis Marschlins, 1793, but this name is a junior synonym for *P. ulyssiponensis*. Notably, another Mediterranean species, *Patella caerulea* Linnaeus, 1758, has been registered at various sites of the Black Sea coast of Turkey [Aydın et al., 2021; Çulha et al., 2007; Güngör, Turan, 2019]. In April 2023, we noted an abundant population of molluscs tentatively identified as *P. ulyssiponensis* in the Sochi port area. It raises a critical question: is it a biological invasion of a Mediterranean species, or is it the recovery of the previously extinct native population of *P. ulyssiponensis* on the Caucasian shelf?

In this study, we clarify the taxonomic identity and discuss the distribution of a gastropod *Patella ulyssiponensis* registered in the Sochi port area. We provide data on the morphological structure and population density of this species as well.

MATERIAL AND METHODS

For laboratory analysis, *P. ulyssiponensis* specimens were sampled on 22 and 26 June, 2023, in the pseudolittoral zone on buoys and breakwaters along the outer side of the southern pier of the Sochi port (station 1) and on a breakwater near the beach of the "Alexandriisky Mayak" apartment complex (station 2). A schematic map of the sampling area is shown in Fig. 1. Molluscs were sampled manually at depths of less than 1 m with a pocketknife and a 25 × 25 cm frame (in triplicate); 144 ind. in total. Live specimens were measured, weighed, and fixed in 70% ethanol. Gastropods were identified down to the species level based on morphological analysis following the papers [Christiaens, 1973; Golikov, Starobogatov, 1972]. Taxa are listed in accordance with the current edition of the WoRMS Editorial Board [2023].

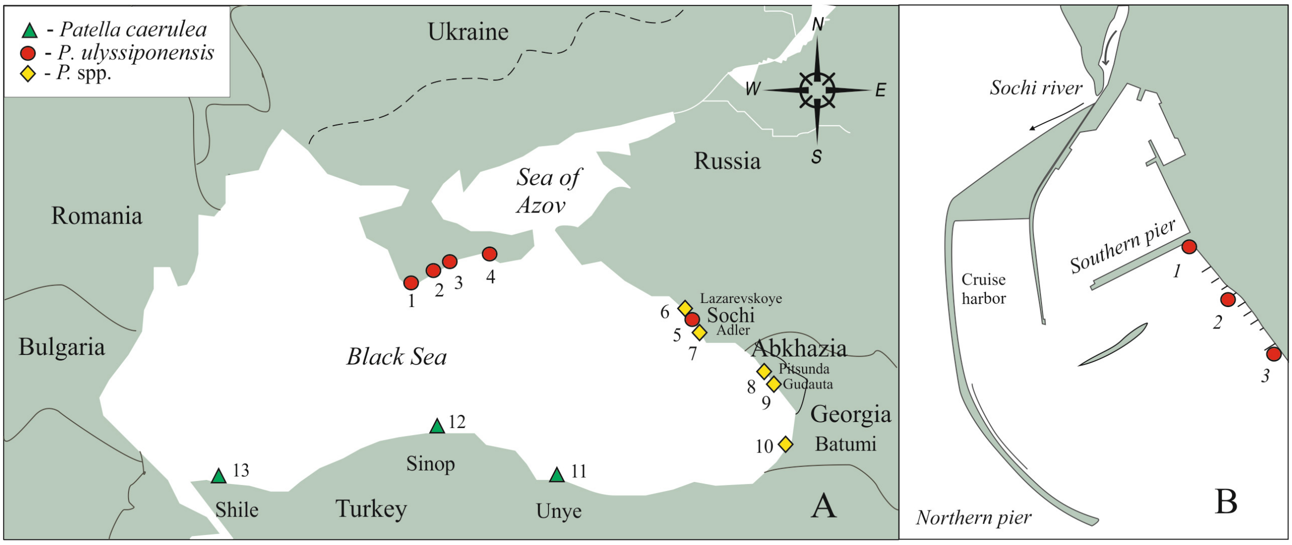

Fig. 1. A, schematic map of records of gastropods of the genus *Patella* in the Black Sea. *Patella ulyssiponensis* (●): 1–4, [Revkov, 2015]; 5, Selifonova *et al.* (our data). *Patella* spp. (♦): 6, 7, Sonicheva L. (Sochi Geographical Society, oral report); 8, 9, Antonova I. (Sochi Geographical Society, oral report); 10, [Kurakin, 2023]. *Patella caerulea* (▲): 11, [Aydın et al., 2021]; 12 — [Çulha et al., 2007]; 13 — [Güngör, Turan, 2019]. B, stations of the mollusc records (1–3) and sampling: 1, outer side of the southern pier of the Sochi port; 2, breakwater near the beach of the "Alexandriisky Mayak" apartment complex

RESULTS

Taxonomic, morphological, and ecological characteristics of molluscs.

Class Gastropoda Cuvier, 1795

Subclass Patellogastropoda Lindberg, 1986

Subfamily Patelloidea Rafinesque, 1815

Family Patellidae Rafinesque, 1815

Genus *Patella* Linnaeus, 1758

Patella ulyssiponensis Gmelin, 1791 (Figs 2, 3).

Material. Sta. 1, 80 ind., shell length of 21.4–43.0 mm. The Black Sea, a buoy, outer side of the southern pier of the Sochi port (N43.578912°, E39.717003°), smooth concrete surface. Fouling: algae of the genera *Ulva*, *Cladophora* (Chlorophyta), *Ceramium*, *Polysiphonia* (Rhodophyta), and *Cystoseira* (Phaeophyta); hydroids (Hydrozoa); sedentary forms of polychaetes of the genus *Spirorbis* (Polychaeta); a bay barnacle *Amphibalanus improvisus* (Darwin, 1854) (Cirripedia); bryozoans (Bryozoa); and bivalves *Mytilus galloprovincialis* Lamarck, 1819 and *Magallana gigas* (Thunberg, 1793) (Bivalvia). At the site of cracks and hollows of the substratum, there were aggregations of small mussels (less than 20–30 mm in length). Samplers: M. Reneva and A. Boran-Keshishyan (22.06.2023).

Sta. 2, 64 ind., shell length of 19.1–35.1 mm. The Black Sea, a breakwater near the beach of the "Alexandriisky Mayak" apartment complex (N43.575430°, E39.723044°), smooth concrete surface. Fouling: algae *U. rigida* (Chlorophyta), *Cystoseira* (Phaeophyta), and a coralline alga

Phymatolithon calcareum (Pallas) W. H. Adey & D. L. McKibbin ex Woelkering & L. M. Irvine, 1986 (Rhodophyta); hydroids (Hydrozoa); sedentary polychaete worms of the genus *Spirorbis* (Polychaeta); a bay barnacle *A. improvisus* (Cirripedia); bryozoans (Bryozoa); a mussel *M. galloprovincialis* (Bivalvia); and a hermit crab *Clibanarius erythropus* (Latreille, 1818) (Decapoda). Samplers: M. Reneva and A. Boran-Keshishyan (26.06.2023).

Fig. 2. Settlement of a gastropod *Patella ulyssiponensis* on the buoys of the Sochi port

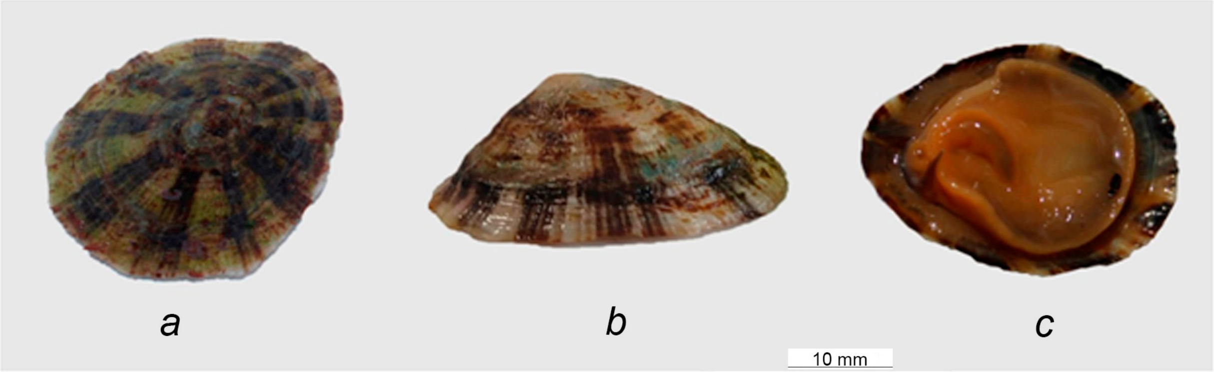

Fig. 3. *Patella ulyssiponensis*: view from above (a); side view (b); view from below (c)

The sampled molluscs are deposited in collections of the Admiral Ushakov Maritime State University (laboratory of marine biology and ecology), the A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS (department of benthic ecology), and the Sochi Geographical Society.

P. ulyssiponensis head and cephalic tentacles are semi-transparent and white, with a yellow buccal disc. The foot is pear-shaped or oval; it is orange, though paler in smaller individuals. The mantle margin is semi-transparent, typically darker than the body, and yellowish-white.

Alternating long and short tentacles of white or yellowish coloration line the mantle margin. In live molluscs, the mantle margin may slightly protrude beyond the shell. In *Patella* individuals studied, the anterior end of the shell was often narrower than the posterior one. The shell apex was centrally positioned or slightly shifted forward.

Externally, the shell exhibits faint ribbing, with an irregular, often serrated edge. Internally, the shell is milky white, occasionally with a bluish tint, and features prominent yellow-orange blotches.

For species identification, we referenced the classic taxonomic revision of the genus *Patella* [Christiaens, 1973]. Diagnostic traits outlined in this paper agree well with subsequent studies. Thus, for specimens from Algerian coastal waters [Beldi et al., 2012], key differences between *P. caerulea* and *P. ulyssiponensis* were rooted in shell morphology, foot coloration, and radula length. *P. caerulea* has a thinner, more rounded shell, with a slightly eccentric apex and a nacreous bluish-gray interior. *P. ulyssiponensis* features a thicker, elongated shell, with a centrally positioned apex and a porcelain-white interior with faint bluish tint. *P. caerulea* exhibits a gray foot sole, while *P. ulyssiponensis* has a yellow-orange one. *P. caerulea* has a radula approximately 1.5 times the shell length, whereas *P. ulyssiponensis* has a shorter radula, roughly equal to the shell in its length [Beldi et al., 2012]. However, other researchers [Christiaens, 1973; Fischer-Piette, 1935; Öztürk, Ergen, 1999] report that differences in radula length between the two species are minimal. This feature is too variable to serve as a reliable diagnostic trait.

These findings agree well with results of *Patella* studies in coastal waters of the Tyrrhenian Sea [Cretella et al., 1994] emphasizing the morphology of soft body parts. According to this paper, *P. caerulea* has a gray head with dark-gray cephalic tentacles and a cream-colored buccal disc. The foot sole is dark-gray along its edge, occasionally with a bluish tint, while the central area is cream-colored. Along the body sides, *P. caerulea* exhibits a mix of long, medium, and short tentacles, with groups of 5–8 alternating medium and short tentacles positioned between 2 long ones. In contrast, *P. ulyssiponensis* features a white head, whitish cephalic tentacles, and a yellow buccal disc. The foot sole is uniformly apricot, yellow, or cream-colored. Along the body sides, there are alternating long and short tentacles only. The results of a comparative analysis of proteins *via* gel electrophoresis carried out in this study and in an earlier paper [Sella et al., 1989] confirm that *P. caerulea* and *P. ulyssiponensis* are closely related species, but separate ones.

The examined individuals were identified as *P. ulyssiponensis* based on the prominence of radial ribs and their grouping into bundles, the position of the shell apex, shell morphometrics, internal shell coloration, integrity or serration of the peristome, soft tissue pigmentation, and the structure of lateral tentacles. Major distinctions between *P. ulyssiponensis* and *P. caerulea* lie in shell morphology and foot sole coloration. As noted above, *P. caerulea* has a thinner and more rounded shell, with a slightly eccentric apex and a nacreous bluish-gray interior. *P. ulyssiponensis*, in contrast, features a thicker and elongated shell, with a centrally positioned apex and a porcelain-white interior, with faint bluish tint. *P. caerulea* has a gray foot sole, while *P. ulyssiponensis* has a yellow-orange one [Beldi et al., 2012]. As for other *Patella* species, *Patella rustica* Linnaeus, 1758 is distinguished by its dark internal shell coloration and brown foot sole, contrasting with the species studied [Beldi et al., 2012]. *Patella vulgata* Linnaeus, 1758 shares the yellow foot sole coloration with *P. ulyssiponensis* (however, it can be gray as well), but differs in gray exterior and yellow-orange interior shell pigmentation [Beldi et al., 2012]. *Patella ferruginea* Gmelin, 1791 also resembles *P. ulyssiponensis* in its yellow-orange foot sole but typically features a gray marginal band. Moreover, *P. ferruginea* possesses long, medium, and short tentacles along the mantle margin. Long tentacles align with radial ribs, while groups of 9–13 alternating medium and short tentacles occupy the space between them [Cretella et al., 1994]. Importantly, *P. ulyssiponensis* exhibits only alternating long and short tentacles. *Patella depressa* Pennant, 1777 differs from the species studied in its gray-black foot sole and orange or brown internal shell coloration [Beldi et al., 2012].

Morphometric population structure. Shell of *P. ulyssiponensis* of the Sochi port area is cap-shaped, relatively thick, and oval (rarely rounded); it has a pointed apex and distinct growth rings. Based on these rings, we can conclude that the age of the molluscs ranged 1 to 5 years. Shell dimensions varied as follows: length, 19.1–43.0 mm; width, 15.2–43.0 mm, and height, 7.0–20.0 mm. Ratios of shell height to its length were (0.43 ± 0.05) and (0.45 ± 0.07) for the first and second habitats investigated, respectively. On average, *P. ulyssiponensis* of the Sochi port area were slightly larger. Detailed morphometric data on the specimens analyzed are provided in Table 1.

Table 1. Morphometric structure of *Patella ulyssiponensis* population ($n = 144$) in the Sochi port area

Parameter	Station 1, outer side of the southern pier of the Sochi port	Station 2, breakwater near the beach of the “Alexandriisky Mayak” apartment complex
Length, mm*	34.4 ± 1.1	26.9 ± 0.5
Min	21.4	19.1
Max	43.0	35.1
Width, mm*	27.9 ± 1.2	21.7 ± 0.5
Min	15.2	17.3
Max	43.0	29.1
Height, mm*	14.5 ± 0.6	12.2 ± 0.3
Min	7.0	8.1
Max	18.1	20.0
Height/length*	0.43 ± 0.05	0.45 ± 0.07
Min	0.33	0.35
Max	0.53	0.62
Weight, m*	5.99 ± 0.5	3.68 ± 0.28
Min	0.9	1.1
Max	10.06	6.67

Note: *, mean ± standard deviation is indicated.

Species population density and weight characteristics. *P. ulyssiponensis* population density ranged within 240–320 ind.$\cdot$m^{-2}, mean of (260 ± 75.7) ind.$\cdot$m^{-2}. Weight varied 3.68 to 5.99 g$\cdot$m^{-2}, mean of (4.8 ± 0.3) g$\cdot$m^{-2}. Density was higher at sta. 1, on the outer side of the southern pier of the Sochi port.

DISCUSSION

Should *P. ulyssiponensis* be considered a Mediterranean biological invader, or do we deal with the recovery of the native Black Sea population? To clarify this issue, we need to analyze the taxonomic status of limpets from the Black and Mediterranean seas. Available literature provides divergent views on the origin of this species. Below, we review up-to-date information supplemented by literature data on *P. ulyssiponensis* biology.

A mollusc *Patella ulyssiponensis* (*P. tarentina* Salis Marschlins, 1793; *P. caerulea* var. *tenuistriata* Weinkauff, 1880 [Ostroumov, 1983]; *P. pontica* Milaschewitsch, 1914; *P. caerulea pontica* Milaschewitsch, 1916 [Il'ina, 1966]) belongs to the class Gastropoda and the family Patellidae (sea limpets) [Golikov, Starobogatov, 1972; Kantor, Sysoev, 2006; Milaschewitsch, 1916; WoRMS, 2023] (see Fig. 3).

In agreement with the classical synopsis of the Black Sea and Sea of Azov fauna [Golikov, Starobogatov, 1972], two *Patella* species inhabited the Black Sea: *P. ferruginea* and *P. tarentina*. The latter one, according to the authors of the synopsis, is closely related to *P. caerulea* and penetrated both the Black Sea and Sea of Azov. Notably, the researchers assert that *P. caerulea* was absent from the Black Sea, even from the Bosphorus area, while both *P. tarentina* and *P. caerulea* inhabit the Mediterranean Sea and the Atlantic coast of Europe as far north as England. They also clarify that *P. ferruginea* had not been recorded in the Black Sea for the last 50 years. Importantly, the genus *Patella* is not mentioned in the monograph on the Sea of Azov molluscs [Anistratenko et al., 2011].

Biodiversity of the Black Sea *Patella* representatives is interpreted quite differently in a later monograph on the Black Sea gastropods [Chukhchin, 1984]. According to this author, only one species (a highly variable one), *P. caerulea*, inhabited the Black Sea; it is considered as an endemic to the Mediterranean Sea.

In contrast, the catalogue of Gastropoda of Russia and adjacent countries [Kantor, Sysoev, 2006] lists three *Patella* species for the Black Sea: *P. caerulea*, *P. ferruginea*, and *P. ulyssiponensis*. There, the latter species is treated as a synonym for *P. tarentina* and is reported for the Sea of Azov as well. As additionally noted, *P. ferruginea* may have become extinct in the Black Sea.

P. ulyssiponensis occurrence in the Black Sea is reported not only by domestic researchers, but also by foreign ones [Katsanevakis et al., 2008]. A recent paper [Gomes et al., 2021] based on genetic and biogeographic studies proves that *P. aspera* Röding, 1798 is a synonym for *P. ulyssiponensis*, although the World Register of Marine Species currently recognizes them as separate species. According to WoRMS [2023], *P. tarentina*, *P. caerulea* var. *tenuistriata*, and *P. pontica* are synonyms for *P. ulyssiponensis*. The latter species, along with *P. caerulea* and *P. ferruginea*, is now considered as a separate and valid one. However, as mentioned above, *P. ulyssiponensis* was often conflated with a highly variable species *P. caerulea*, a Mediterranean endemic [Chukhchin, 1984]. Thus, the assumption about the independent status of *P. ulyssiponensis* and its occurrence in the Black Sea can now be considered as well-supported and proved.

Morphometric analysis of shell structure is crucial for mollusc taxonomy. The specimens we examined were generally smaller, but had higher shells compared to those from the Black Sea population and a population of the northern Aegean Sea (the Gulf of Saros), where *P. ulyssiponensis* had an average shell length of 36.4 mm (maximum of 48.6 mm), width of 28.9 mm, and height of 9.5 mm [Öztürk, Ergen, 1999]. According to [Golikov, Starobogatov, 1972], the Black Sea specimens can reach the length of 45.0 mm, width of 30.0 mm, and height of 14.0 mm. Flatter shells of Mediterranean *Patella* representatives compared to the Black Sea molluscs are known for a long time and are typical of limpets inhabiting the intertidal zone [Chukhchin, 1984]. Thus, the Black Sea *P. ulyssiponensis* have some morphological distinctions from the Mediterranean Sea ones. This raises the question of whether the differences reflect intraspecific variability, or it is reasonable to consider the Black Sea populations of *P. ulyssiponensis* as a separate subspecies or even species.

We found no published data on *P. ulyssiponensis* reproduction and development. However, based on what is known about *P. caerulea* [Aydın et al., 2021; Chukhchin, 1984; Ferranti et al., 2018; Wanninger et al., 1999a, b], it is plausible to infer that *P. ulyssiponensis* is also a perennial polycyclic species with protandric hermaphroditism and a short planktonic larval stage. Its reproduction likely occurs in autumn (in October and November), the same as in *P. caerulea*.

Like other representatives of the genus, *P. ulyssiponensis* feeds by scraping bacterial–algal films from rocks. Also, literature data [Ayas, 2010; Silva et al., 2008] evidence for the fact that this mollusc feeds on multicellular green algae, *Ulva lactuca* Linnaeus, 1753 in particular. However, its primary diet is thought to consist of red coralline algae, chiefly *Ellisolandia elongata* (J. Ellis et Solander) K. R. Hind et G. W. Saunders, 2013 frequently noted in literature under its former name, *Corallina elongata* J. Ellis et Solander, 1786. Pigments from red algae may impart an orange tint to inner layers of *P. ulyssiponensis* shells. This species is reported [Branch, 1981; Katsanevakis et al., 2008] as a territorial one. After foraging, adults consistently return to their habitats, where deep depressions can be formed due to localized erosion of underlying soft coralline algae. However, research by M. Seabra *et al.* [2019] did not support the hypothesis that *P. ulyssiponensis* larvae preferentially settle on red coralline algae substrates. Laboratory-reared larvae showed similar settlement rates on concrete and stone surfaces. These biological traits suggest that adult *P. ulyssiponensis* are unlikely to migrate from rocky substrates to ship hulls or keels and thus be transported to other areas. Interestingly, settling of larvae on submerged ship surfaces could enable dispersal to new sites: if larvae mature and release fertilized eggs en route, this might facilitate colonization of previously unoccupied water areas.

Regarding the ecology of prosobranchs with short pelagic larval phase, such as *P. ulyssiponensis*, it should be noted as follows: *Patella* species are inhabitants of contour biotopes. These crawling gastropods inhabit hard-substrate communities in the mid-littoral, upper infra-littoral, and partly supralittoral zones along temperate Eastern Atlantic and Mediterranean coasts [Vafidis et al., 2020]. *P. ulyssiponensis* prefers rocky shores with wave exposure levels ranging 1 to 4–5 on the Beaufort scale [Ballantine, 1961], where water turbidity does not impede algal growth. The species is common on open or semi-open coasts, while in sheltered bays, its abundance declines. The primary limiting factor for molluscs is coastal pollution, particularly by toxic surfactants, *inter alia* petroleum derivatives [Black Sea Red Data Book, 1999]. Anthropogenic load is increasing and more and more affecting coastal ecosystems, in particular altering *Patella* habitats and population structures. In the Sochi Port area, *P. ulyssiponensis* settlements were recorded on smooth concrete surfaces (on a buoy and tetrapods) predominantly colonized by green, red, and brown algae, as well as by oysters and mussels. A red coralline alga, typically associated with the primary habitat of this species, was observed rarely – only on a breakwater near the beach of the “Alexandriisky Mayak” apartment complex (sta. 2). Notably, the outer side of the southern pier (sta. 1) hosting a more abundant population benefits from water exchange with the open sea and full-depth water clarity. This station is far from a more polluted semi-enclosed port water area, where transparency is limited to 1–2 m and the seabed consists of silty black sediments emitting a strong hydrogen sulfide odor (see Fig. 1). Improved habitat conditions along the Sochi coast have facilitated *P. ulyssiponensis* distribution in the region.

The occurrence of the population of this species on the Caucasian shelf can be driven by the recovery of the Black Sea ecosystem following a period of eutrophication, with reduced pressure from planktonic predators (the warty comb jelly *M. leidyi*), reduction and shrinkage of the population of the rapa whelk

Rapana venosa (Valenciennes, 1846), and with a shift in climate conditions [Arashkevich et al., 2015; Pereladov, 2013; Sayenko, Marushko, 2018]. Analysis of literature data suggests a current trend toward the recovery of the limpet populations in the southern Black Sea (on the Turkish coast) as well [Aydın et al., 2021; Güngör, Turan, 2019].

Potential pathways of *Patella ulyssiponensis* dispersal in the Black Sea. Currently, *P. caerulea* is recorded in various areas off the Black Sea coast of Turkey [Aydın et al., 2021; Çulha et al., 2007; Güngör, Turan, 2019]. Genetic and morphological analysis and studies of reproductive traits were carried out for this species [Aydın et al., 2021; Güngör, Turan, 2019]. Comparative DNA analysis revealed closely related haplotypes in *P. caerulea* individuals inhabiting the port of Şile area (coast of Turkey) and the Sea of Marmara. According to [Güngör, Turan, 2019], the greatest divergence was observed between the Black Sea population and the Mediterranean one. In the Mediterranean basin, five limpet species are documented: *P. caerulea*, *P. rustica*, *P. ulyssiponensis*, *P. ferruginea*, and *P. depressa*; out of them, only *P. caerulea* is an endemic one [Mauro et al., 2003]. As noted earlier, *P. ulyssiponensis* we studied features significant morphological differences from other Mediterranean *Patella* species. Considering this, we hypothesize substantial genetic divergence between the Black Sea *P. ulyssiponensis* population and the Mediterranean one.

It remains unclear, how did *P. ulyssiponensis* reach the northeastern Caucasian shelf if it has not been recorded along the Black Sea coast of Turkey. Importantly, its absence in published material and in a mollusc collection of the Sochi Geographical Society assembled in the 1960s evidences for the fact that this species disappeared from the Caucasian shelf of the Black Sea in the middle of the XX century. The staff of the Admiral Ushakov Maritime State University carried out summer benthic surveys with scuba diving equipment in the areas of the Sochi port, Khosta breakwaters, and Cape Vidny in 2012–2013 and in Sukhumi port area in 2016–2017 [Selifonova, 2018; Selifonova, Bartsits, 2018; Selifonova et al., 2019]. There were no *P. ulyssiponensis* in fouling communities of piers, breakwaters, rocks, and stones. Since 2012–2014, as already mentioned, researchers from the Sochi Geographical Society registered single *Patella* spp. along the coast from Lazarevskoye to Adler (L. Sonicheva and I. Antonova, oral reports). In 2019–2020, the authors observed a noticeable aggregation of the mollusc not only in Sochi vicinity, but also in Abkhazia, along Pitsunda and Gudauta coasts. Based on shell age analysis, we can conclude as follows: *P. ulyssiponensis* has been spreading along the entire Sochi coast from Adler to Lazarevskoye since approximately 2017–2018. Along the Georgian coast, south of Batumi, *Patella* spp. was recorded in 2017 [Kurakin, 2023].

Let us discuss potential pathways of dispersal (introduction vectors) of this mollusc in the shelf zone of the Caucasian Black Sea coast.

One hypothesis (considering *P. caerulea* finding on the Black Sea coast of Turkey) covers *P. ulyssiponensis* reinvasion from the Mediterranean Sea. Apparently, this transfer of the limpet occurred similarly to the introduction of a gastropod *R. venosa*. According to a widely accepted hypothesis, the rapa whelk was introduced to the Black Sea in the 1940s *via* a ship with a hull carrying its egg cases. An alternative pathway has also been proposed: transport *via* ballast water of ships [Pereladov, 2013]. The same as with *R. venosa*, after *P. ulyssiponensis* introduction to the Black Sea, its morphological and biological characteristics may gain variability under new ecological conditions.

Our study does not dismiss the hypothesis of the limpet transfer *via* fouling of plastic hulls of yachts and boats. An adult specimen could be transported by a passenger vessel if a mollusc was attached to the submerged ship surface. Sochi hosts the largest passenger port on the Black Sea specializing in cruises to the Black Sea and Mediterranean countries and republics: Abkhazia, Egypt, Georgia, and Turkey (until recently, to Cyprus, Greece, and Israel as well). The Sochi port covers the main seaport in Sochi, eight marine terminals (Imeretinka, Adler, Kurortny, Khosta, Matsesta, Dagomys, Loo, and Lazarevskoye), and the cargo area of the seaport, Sochi Imeretinsky, at the Mzymta River mouth. In literature, just one case of introduction has been described (the only one so far): from the deepwater commercial port of Sines on the Atlantic coast of Portugal [Seabra et al., 2008]. There, a hypothesis was tested in 2005 about different distribution models for *Patella* molluscs on natural rocky substrates outside the port and artificial tidal pools within the port area. Experimentally, the highest density of settled larvae was observed on plastic (on PVC panels). Some researchers report the limpet introduction far beyond marine basins. For example, a lake-type rounded shell of *P. ulyssiponensis*, about 4–5 years old, was washed ashore on a deserted bank of the Volga River in autumn 2022 (the Kuybyshev Reservoir, Ulyanovsk) [Artemyeva, Semenov, 2022]. The authors suggest that the mollusc could have been transported on hulls of river/sea vessels navigating the Volga – Don – Sea of Azov – Black Sea – Mediterranean Sea waterway.

Another potential vector for *P. ulyssiponensis* dispersal is larval transfer *via* coastal currents and ballast water of merchant ships. However, this hypothesis is debatable due to the lecithotrophic larval stage of the limpet which has a short developmental phase. The most plausible scenario is as follows: adult molluscs reached the Caucasian shelf of the Black Sea within enclosed ballast water volumes of ships transporting containers and bulk cargo through the Sochi Imeretinsky area during the construction of the Olympic Park facilities and later (in 2010–2022). Along the Caucasian coast, the Rim Current flows east to west enabling *P. ulyssiponensis* to subsequently spread along the entire Sochi coastline. During summer, catamarans, passenger ships, and recreational boats operate between Sochi and Abkhazia (Sukhumi and Gagra). Accordingly, there is the question: what are potential limits for further limpet expansion in the Black Sea?

Despite existing diagnostic keys, *P. ulyssiponensis* morphological identification remains pretty challenging, as distinguishing traits within the genus are unreliable. This underscores the need for molecular-genetic methods [Sanna et al., 2012]. Those have already confirmed that *P. caerulea* and *P. ulyssiponensis* are separate species *via* comparison of mitochondrial DNA [Sá-Pinto et al., 2005]. The species also differ in chromosome morphology and number: *P. ulyssiponensis* has a haploid set of 8 ones, while *P. caerulea* has 9 [Petraccioli et al., 2010]. Given the pronounced morphological variability of *P. ulyssiponensis* in the Black and Mediterranean seas, only comprehensive genetic analysis can clarify its taxonomic status: is it a species, subspecies, ecomorph, or a case of individual variability.

Conclusions. Based on a literature review of morphological features, biology, and ecology of the Black Sea and Mediterranean *Patella* representatives, as well as analysis of our own material sampled in June 2023, we conclude that an abundant population found in the Sochi port area belongs to the species *Patella ulyssiponensis*.

We assume that the limpet occurrence within the northeastern Caucasian Black Sea shelf is associated with anthropogenic transfer by ships and its subsequent natural dispersal in the region. However, the possibility of a natural recovery of a previously existing local population cannot be ruled out. Available data do not allow a definitive choice to be made between these two hypotheses. A precise determination of *P. ulyssiponensis* occurrence in this area requires comparative genetic studies of *Patella* populations inhabiting the Black Sea off the Caucasian shores and coast of Turkey. The observed abundant aggregation of the limpet on the Caucasian shelf may be attributed to the recovery of the Black Sea ecosystem following a period of eutrophication, reduced pressure from planktonic and benthic predators (the warty comb jelly *Mnemiopsis leidyi* and the rapa whelk *Rapana venosa*, respectively), and a shift in climate conditions.

Despite the emerging trend of *P. ulyssiponensis* population recovery at one site (along the Caucasian coast in the Sochi port area), long-term ecological effects of its historical decline persist in other Black Sea regions (the Crimea, Ukraine, Bulgaria, and Romania). There, *Patella* representatives remain rare, endangered species. Consequently, due to its conservation status and absence in several coastal zones of the Black Sea, *P. ulyssiponensis* cannot currently be considered a target for commercial harvesting.

Nevertheless, this finding, along with other recent observations, highlights positive shifts in gastropod fauna of the Caucasian Black Sea area.

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БРЮХОНОГИЙ МОЛЛЮСК *PATELLA ULYSSIPONENSIS* GMELIN, 1791 (GASTROPODA: PATELLIDAE) НА КАВКАЗСКОМ ШЕЛЬФЕ ЧЁРНОГО МОРЯ: БИОЛОГИЧЕСКАЯ ИНВАЗИЯ ИЛИ ВОССТАНОВЛЕНИЕ НАТИВНОЙ ПОПУЛЯЦИИ?

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Весной 2023 г. в районе Сочинского порта обнаружена многочисленная популяция, состоящая из взрослых особей брюхоногого моллюска *Patella ulyssiponensis* Gmelin, 1791. *P. ulyssiponensis*, так называемое морское блюдечко, — контуробионт, ползающий съедобный брюхоногий моллюск; он занесён в Красную книгу Чёрного моря, Крыма и Севастополя и до сих пор отсутствует на шельфе Крыма, Украины, Румынии, Болгарии и Турции. На кавказском шельфе моллюска не находили примерно с середины XX в. В работе приведены данные о распространении, морфологической структуре и плотности поселения моллюсков *P. ulyssiponensis*, собранных в районе Сочинского порта в июне 2023 г. По выраженности радиальных рёбер и их объединению в пучки, положению макушки, морфометрии самой раковины, цвету внутренней поверхности раковины, а также цельности или зубчатости перистомы обнаруженный нами вид был отнесён к *P. ulyssiponensis*, который известен в Чёрном море как *Patella tarentina* Salis Marschlins, 1793, *P. caerulea* var. *tenuistriata* Weinkauff, 1880 и *P. pontica* Milaschewitsch, 1914 (syn.). В более ранних работах по Чёрному морю его объединяли с *P. caerulea* Linnaeus, 1758 — эндемиком Средиземного моря. Плотность *P. ulyssiponensis* в районе Сочинского порта достигала 240–320 экз.$\cdot$м$^{-2}$

и была выше на станции, расположенной на внешней стороне южного мола, чем в районе пляжей. Изученные нами особи были несколько мельче ранее отмеченных в Чёрном море. Максимальная длина раковины в районе исследования достигала 43,0 мм, ширина — 17,3 мм, высота — 20 мм. Особи из района Сочи имели более высокую раковину, чем особи черноморской популяции и популяции из северной части Эгейского моря, что характерно для обитателей уреза воды. Для первого и второго исследованного местообитания отношение высоты раковины к её длине составляло (0,43 ± 0,05) и (0,45 ± 0,07) соответственно. Реинвазия *P. ulyssiponensis* в северо-восточную часть кавказского шельфа могла быть связана с антропогенным переносом судами и с естественным расселением. Это открытие, наряду с другими аспектами, отмеченными в последние годы в экосистеме Чёрного моря, иллюстрирует позитивные изменения в фауне брюхоногих моллюсков кавказского шельфа.

Ключевые слова: *Patella ulyssiponensis*, распространение, морфометрия, плотность, Сочинский порт

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THE INFLUENCE OF WATER SALINITY ON THE DISTRIBUTION OF MYXOSPOREANS OF THE GENUS *KUDOA* (CNIDARIA, MYXOZOA) AMONG FISH OF THE WORLD FAUNA

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The occurrence of myxosporeans of the genus *Kudoa* in fish inhabiting waters of different salinity was studied. The work is based on own materials on fish myxosporeans sampled in 1987–2021: more than 12,000 specimens of about 100 fish species in the basins of the Atlantic Ocean [the Sea of Azov (Russia and Ukraine), Black Sea (Russia, Ukraine, and Turkey), and Mediterranean Sea (Italy and Spain); the Central Eastern Atlantic (abeam Mauritania) and southern latitudes off the coast of Africa (abeam Namibia); waters of the northern (near Norway) and southern (abeam Argentina) parts of the ocean; and off the southeastern coast of the USA], the Indian Ocean [the coast of Yemen], and the Pacific Ocean [South China Sea (Vietnam)]. In total, 27 representatives of myxosporeans of the genus *Kudoa* were analyzed using original material; out of them, 19 were identified down to the species level. Also, all available literature sources and a global database of fish species FishBase were investigated. As established, out of 291 species of fish hosting *Kudoa*, 169 species are exclusively marine, 76 species can inhabit marine- and brackish-water environments, 42 species are euryhaline and can occur both in marine and brackish waters and in freshwater, and only 4 species are exclusively freshwater ones. Out of 128 *Kudoa* species, 117 (91.4%) were found in the marine zone of the World Ocean; 8 (6.3%), in its estuaries (7, in marine fish; 1, in a freshwater host); and 3 (2.3%), in freshwater reservoirs. In 2008–2019, *Kudoa nova* Naidenova, 1975 was studied in estuarine-type ecosystems off the coast of the Crimea at the Chernaya River mouth and Karkinitsky Bay (the Black Sea), as well as in Eastern Sivash (the Sea of Azov). A total of 2,232 specimens of 11 goby species were examined. As established, the periodic desalination of some areas by waters of paddy fields and the constant occurrence of freshwater in a surface layer of the Chernaya River mouth did not cause a noticeable change in salinity (except for the northern area of Eastern Sivash) which would be destructive for this parasitic species. However, there were no *K. nova* in gobies caught in 1998 in the Taganrog Bay (the Sea of Azov) significantly desalinated by the Don River water. Also, this species was not recorded in 2011 in the Bug and Vistula rivers when studying microparasites of gobies that spread from the northwestern Black Sea along the central invasive corridor. Our experiment testified to the negative influence of freshwater on spores of this parasite: under its effect, spores were deformed and darkened, and the function of the polar filament extrusion was disrupted.

Keywords: myxosporeans, *Kudoa*, water salinity, world fauna

One of the key ecological factors of the external environment (second-order environment) significantly affecting fish infestation by certain myxosporeans is salinity of water where fish and, periodically, their parasites occur. This is evidenced by the clear division of all myxosporean species into marine and freshwater ones [Shulman et al., 1997]. This monograph thoroughly examines the issue on examples of both freshwater and marine species not belonging to the genus *Kudoa* Meglitsch, 1947. An exception is *K. nova* Naidenova, 1975 reported as a marine species found in desalinated waters of the Sea of Azov. The researchers emphasize the qualitative and quantitative depletion of myxosporean fauna in marine basins within their brackish spots and adverse effects of increased salinity on diversity and abundance of exclusively freshwater species in freshwater habitats (it is entirely expected). A group of euryhaline fish hosts is highlighted whose myxosporeans typically originate from both marine and freshwater environments. They can inhabit zones of various salinity and should be classified as brackish-water species. According to S. Shulman [1966], such hosts act as a sort of 'artificial climate compartment' for parasites. The relative ease with which certain myxosporeans shift between marine and freshwater environments and backwards is associated not only with the presence of euryhaline hosts, but also with protective properties of spore valves in Myxosporea that shield an amoeboid embryo from harmful effect of environment.

In earlier work, we explored the effect of salinity on infestation of the Black Sea fish by myxosporeans of other genera [Yurakhno, 1994]. We also reported a gradual depletion of marine myxosporean fauna and replacement by freshwater elements when moving from west to east, from the Black Sea to the Caspian Sea. This trend is accompanied by a significant reduction in myxosporean species diversity in fish of the Sea of Azov and Caspian Sea as compared to that for the Black Sea [Yurakhno, 1994; Yurakhno, Özer, 2018, 2020].

Analyzing the world fauna of *Kudoa* myxosporeans comprehensively outlined in the latest synopsis of species [Eiras et al., 2014], we confirmed this pattern on the example of representatives of this genus. Thus, five *Kudoa* species are registered in the Black Sea [*K. anatolica* Özer, Okkay, Gurkanlı, Çiftci & Yurakhno, 2018, *K. niluferi* Özer, Okkay, Gurkanlı, Çiftci & Yurakhno, 2018, *K. nova*, *K. stellula* V. Yurakhno, 1991, and *K. quadratum* (Thélohan, 1895)], while only two are recorded in the Sea of Azov [*K. nova* and *K. dicentrarchi* Sitjà-Bobadilla & Alvarez-Pellitero, 1992]. Notably, there are no *Kudoa* species in the Caspian Sea. At first glance, the negative effect of desalination seems evident supporting the earlier opinion that the entire order Multivalvulida to which *Kudoa* belongs covers exclusively marine forms [Shulman et al., 1997]. However, recent investigations have revealed rare facts of *Kudoa* infecting freshwater fish not only in lagoons [Fomena, Bouix, 1997; Siau, 1971] or estuaries [Sarkar, Chaudhury, 1996], but also in a river connected to the Atlantic Ocean [Azevedo et al., 2016; Casal et al., 2008; Velasco et al., 2015]. The effect of salinity on *Kudoa* infestation of fish has not been systematically analyzed in literature, aside from carrying out experiments on survival of *K. nova* spores [Yurakhno, 2015b, 2016a, 2018] and *Kudoa septempunctata* Matsukane, Sato, Tanaka, Kamata & Sugita-Konishi, 2010 spores [Yokoyama et al., 2016] in freshwater and saline water, as well as our own studies on myxosporean fauna in Crimean estuarine zones. Results on the latter ones are published only in conference abstracts and proceedings [Dmitrieva et al., 2015; Korniichuk et al., 2016; Yurakhno, 2012, 2013, 2014, 2015a, 2016b; Yurakhno, Tokarev, 2017]. To fill this gap, we aimed at providing comprehensive insights into the issue.

MATERIAL AND METHODS

This study is based on our own original data on fish myxosporeans sampled in 1987–2021. Over 12,000 specimens of approximately 100 fish species were examined in the basins of the Atlantic Ocea [the Sea of Azov (Russia and Ukraine), Black Sea (Russia, Ukraine, and Turkey), and Mediterranean Sea (Italy and Spain); the Central Eastern Atlantic (abeam Mauritania) and southern latitudes off the coast of Africa (abeam Namibia); waters of the northern (near Norway) and southern (abeam Argentina) parts of the ocean; and off the southeastern coast of the USA], the Indian Ocean [the coast of Yemen], and the Pacific Ocean [South China Sea (Vietnam)]. In total, 27 *Kudoa* representatives were identified based on original material; this covers 19 ones identified down to the species level [*K. alliaria* Kovaleva, Shulman & Yakovlev, 1979, *K. anatolica*, *K. borimiri* Yurakhno, Slynko, Nguyen, Vo & Whipps, 2022, *K. clupeidae* (Hahn, 1917), *K. dicentrarchi*, *K. histolytica* (Pérard, 1928) Meglitsch, 1947, *K. igori* Yurakhno, Slynko, Nguyen, Vo & Whipps, 2022, *K. inornata*, *K. mirabilis* Naidenova & Gaevskaya, 1991, *K. monodactyli* Gunter, Cribb, Whipps & Adlard, 2006, *K. niluferi*, *K. nova*, *K. paniformis* Kabata & Whitaker, 1981, *K. rosenbuschi* (Gelormini, 1943), *K. stellula*, *K. thyrsites* (Gilchrist, 1924) Meglitsch, 1947, *K. trifolia* Holzer, Blasco-Costa, Sarabeev, Ovcharenko & Balbuena, 2006, *K. unicapsula* Yurakhno, Ovcharenko, Holzer, Sarabeev & Balbuena, 2007, and *K. whippsi* Burger & Adlard, 2010] and 8 *Kudoa* spp. Additionally, descriptions of 128 *Kudoa* species documented in global scientific literature up to 2021 were analyzed. To assess *Kudoa* occurrence in fish inhabiting waters of various salinity, we referenced FishBase (https://www.fishbase.se/search.php) verifying data in available sources [Debelius, 2009; Fadeev, 2005; Svetovidov, 1964; The Living Marine Resources, 2016].

For the salinity-dependent infestation analysis of gobies by *K. nova*, we examined 2,232 specimens of 11 fish species in 1998 and 2008–2019. Sampling sites included estuarine biotopes of the Black Sea and Sea of Azov and the central invasive corridor connected to the Black Sea (Bug, Narew, and Vistula rivers in Poland).

For water samples from the Karkinitsky Bay (2014–2016), salinity was measured *via* argentometry (the guiding document RD 52.10.243-92, Manual of Chemical Analysis of Marine Waters, 01.07.1993) by T. Bogdanova (IBSS). Salinity data for 2008–2013 in this region were provided orally by N. Shadrin (IBSS). Sivash Lagoon salinity was sourced from oral report by A. Boltachev (IBSS) (measurements were carried out by T. Bogdanova) and from the paper [Shadrin et al., 2018]. Data on the Taganrog Bay salinity in 1998 were provided by AzNIIRKh researchers. Salinity values for the Vistula and Bug rivers were derived from literature [Kasprzak et al., 2016] and from an online source (https://en.wikipedia.org/wiki/Bug_(river)), respectively, with lower water salinity thresholds for the Bug River provided by N. Ovcharenko (the W. Stefański Institute of Parasitology of the PAS, Warsaw, Poland). Data on salinity in the Dnieper–Bug estuary were sourced from literature [Grinevetsky et al., 2015].

RESULTS AND DISCUSSION

When analyzing all *Kudoa* hosts by their ability to survive in water of various salinity (Table 1), it becomes evident that the overwhelming majority of *Kudoa* myxosporeans parasitize marine fish inhabiting seas and oceans. Out of 294 fish hosts for *Kudoa*, habitat preferences were determined for 291 species. Out of them, 169 species are exclusively marine, 76 can inhabit marine- and brackish-water environments, 42 are euryhaline and can occur both in marine and brackish waters and in freshwater, and only 4 are exclusively freshwater ones. For 3 fish hosts with unresolved taxonomic status, habitat preferences could not be established.

Most *Kudoa* species were registered in marine zones of the World Ocean confirming the marine origin of this genus. Exceptions cover four *Kudoa* found in freshwater fish from freshwater basins adjacent to the Atlantic Ocean. Out of them, three were reported from fish of the order Cichliformes –

from *Aequidens plagiozonatus* Kullander, 1984 (*Kudoa aequidens* Casal, Matos E., Matos P. & Azevedo, 2008) [Casal et al., 2008] and *Chaetobranchopsis orbicularis* (Steindachner, 1875) (*Kudoa orbicularis* Azevedo, Rocha, Matos, Oliveira, Matos, Al-Quraishy & Casal, 2016) [Azevedo et al., 2016] – and from fish of the order Siluriformes – from *Hypophthalmus marginatus* Valenciennes, 1840 (*Kudoa* sp.) [Velasco et al., 2015] – in the lower Amazon River basin (Brazil). Interestingly, *K. orbicularis* was found in the Arari River, 135 km from the Amazon River mouth. And the fourth species (*Kudoa eleotrisi* Siau, 1971) was noted in a sleeper goby *Kribia kribensis* (Boulenger, 1907) in the Porto-Novo Lagoon (Benin, coast of Africa) [Fomena, Bouix, 1997; Siau, 1971]. *Kudoa cascasia* Sarkar & Chaudhury, 1996 was recorded in the freshwater yellowtail mullet *Minimugil cascasia* (Hamilton, 1822) in the Hooghly estuary (the Indian Ocean, Western Bengal, India) [Sarkar, Chaudhury, 1996].

Table 1. Occurrence of myxosporeans of the genus *Kudoa* in fish of various taxa of the world fauna, with indication of the affiliation of hosts to waters of different salinity*

Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Class Chondrichthyes **Subclass Elasmobranchii** **Superorder Selachomorpha**		
Order Carcharhiniformes		
Family Carcharhinidae		
Carcharhinus amboinensis	M, B	*K. carcharhini*
C. cautus	M	*K. carcharhini*
C. limbatus	M, B	*K. carcharhini*
Order Orectolobiformes		
Family Hemiscylliidae		
Hemiscyllium ocellatum	M	*K. hemiscylli*
Family Orectolobidae		
Orectolobus hutchinsi	M	*K. hemiscylli*
O. maculatus	M	*K. hemiscylli*
O. ornatus	M	*K. hemiscylli*
Suborder Batomorpha		
Order Myliobatiformes		
Family Dasyatidae		
Hemitrygon fluviorum	M, B	*K. hemiscylli*
Neotrygon kuhlii	M	*K. hemiscylli*
Taeniura lymma	M	*K. hemiscylli*
Order Rhinopristiformes		
Family Rhinobatidae		
Aptychotrema rostrata	M, B	*K. hemiscylli*
Glaucostegus typus	M, B, Fr	*K. hemiscylli*
Class Actinopterygii **Infraclass Teleostei**		
Order Carangaria incertae sedis		
Family Sphyraenidae		
Sphyraena jello	M, B	*K. sphyraeni*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
S. pinguis	M	*K. megacapsula*
S. putnamae	M	*K. barracudai*
Order Eupercaria incertae sedis		
Family Gerreidae		
Eugerres brasilianus	M	*K. eugerres*
Family Labridae		
Coris julis	M	*K. quadratum*
Halichoeres bivittatus	M	*K. ovivora*
H. garnoti	M	*K. ovivora*
H. poeyi	M	*K. ovivora*
Tautogolabrus adspersus	M	*K. clupeidae*
Thalassoma bifasciatum	M	*K. ovivora*
Th. lunare	M	*K. thalassomi*
Th. lutescens	M	*K. thalassomi*
Family Lethrinidae		
Gymnocranius audleyi	M	*K. lethrini*
Lethrinus harak	M, B	*K. lethrini*
L. nebulosus	M, B	*K. iwatai*
L. variegatus	M	*K. iwatai*
Family Lutjanidae		
Caesio cuning	M	*K. chaetodoni*
Lutjanus campechanus	M	*K. hypoepicardialis*
L. carponotatus	M	*K. chaetodoni*
L. ehrenbergii	M, B, Fr	*K. lethrini*, *K. yasunagai*
L. erythropterus	M	*K. iwatai*, *K. lutjanus*
L. fulviflamma	M	*K. lethrini*
L. lemniscatus	M	*K. lemniscati*
Family Monodactylidae		
Monodactylus argenteus	M, B, Fr	*K. monodactyli*
Family Moronidae		
Dicentrarchus labrax	M, B, Fr	*K. dicentrarchi*, *K. iwatai*
D. punctatus	M, B	*K. dicentrarchi*
Family Nemipteridae		
Nemipterus japonicus	M	*K. schulmani*
Scolopsis monogramma	M	*K. yasunagai*
Family Priacanthidae		
Priacanthus hamrur	M	*K. iwatai*
Family Scaridae		
Calotomus japonicus	M	*K. igami*, *K. lateolabracis*, *K. thalassomi*, *K. yasunagai*
Scarus flavipectoralis	M	*K. thalassomi*
Sparisoma aurofrenatum	M	*K. ovivora*
S. radians	M	*K. ovivora*
S. rubripinne	M	*K. ovivora*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Family Sciaenidae		
Cheilotrema fasciatum	M	*K. sciaenae*
Cynoscion nebulosus	M, B	*K. inornata*
Leiostomus xanthurus	M, B	*K. branchiata*, *K. leiostomi*
Nibea coibor	M, B	*K. coibori*
Paralonchurus peruanus	M	*K. sciaenae*
Pogonias cromis	M, B	*K. hypoepicardialis*
Sciaena deliciosa	M	*K. sciaenae*
Stellifer minor	M	*K. sciaenae*
Family Sillaginidae		
Sillago analis	M, B	*K. ciliatae*
S. ciliata	M, B	*K. ciliatae*, *K. yasunagai*
S. maculata	M, B	*K. ciliatae*, *K. yasunagai*
S. sihama	M, B	*K. petala*
Family Sparidae		
Acanthopagrus latus	M, B, Fr	*K. lutjanus*
A. schlegelii	M, B	*K. iwatai*
Argyrops filamentosus	M	*K. iwatai*
Boops boops	M	*K. boopsi*
Dentex macrophthalmus	M	*K. nova*
Pagellus acarne	M	*K. nova*
Pagrus major	M	*K. iwatai*, *K. yasunagai*
P. pagrus	M	*K. pagrusi*
Rhabdosargus haffara	M	*K. aegyptia*
Sparus aurata	M, B	*K. dicentrarchi*, *K. iwatai*
Stenotomus chrysops	M	*K. clupeidae*
Order Ovalentaria incertae sedis		
Family Pomacentridae		
Abudefduf bengalensis	M	*K. amamiensis*, *K. thalassomi*, *K. whippsi*
A. septemfasciatus	M	*K. gunterae*
A. sexfasciatus	M	*K. amamiensis*, *K. gunterae*
A. sordidus	M, B	*K. gunterae*
A. vaigiensis	M	*K. amamiensis*, *K. whippsi*
A. whitleyi	M	*K. amamiensis*, *K. thalassomi*, *K. whippsi*
Acanthochromis polyacanthus	M	*K. whippsi*
Amblyglyphidodon curacao	M	*K. thalassomi*
Amphiprion akindynos	M	*K. kenti*, *K. thalassomi*, *K. whippsi*
A. melanopus	M	*K. kenti*, *K. thalassomi*, *K. whippsi*
Chromis chrysura	M	*K. amamiensis*
Ch. notata	M	*K. amamiensis*
Ch. viridis	M	*K. gunterae*, *K. whippsi*
Chrysiptera assimilis	M	*K. amamiensis*
C. cyanea	M	*K. gunterae*, *K. thalassomi*
Dascyllus aruanus	M	*K. gunterae*, *K. thalassomi*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
D. trimaculatus	M	*K. iwatai*
Dischistodus perspicillatus	M, B	*K. kenti*
D. pseudochrysopoecilus	M	*K. gunterae*
Neoglyphidodon melas	M	*K. gunterae*, *K. thalassomi*, *K. whippsi*
Neopomacentrus miryae	M	*K. iwatai*
Plectroglyphidodon leucozonus	M	*K. gunterae*, *K. kenti*
Pomacentrus chrysurus	M	*K. gunterae*, *K. whippsi*
Order Acanthuriformes		
Family Chaetodontidae		
Chaetodon baronessa	M	*K. thalassomi*
C. collare	M	*K. muscularis*
C. paucifasciatus	M	*K. iwatai*
C. unimaculatus	M	*K. chaetodoni*, *K. thalassomi*
C. vagabundus	M	*K. thalassomi*
Chelmon rostratus	M, B	*K. thalassomi*
Heniochus monoceros	M	*K. thalassomi*
Family Leiognathidae		
Leiognathus brevirostris	M, B	*K. uncinata*
Nuchequula nuchalis	M, B	*K. uncinata*
Family Lobotidae		
Lobotes surinamensis	M, B	*K. hypoepicardialis*
Family Siganidae		
Siganus rivulatus	M, B	*K. iwatai*
Order Acropomatiformes		
Family Lateolabracidae		
Lateolabrax japonicus	M, B, Fr	*K. cruciformum*, *K. iwatai*, *K. yasunagai*
Lateolabrax sp.	?	*K. lateolabracis*
Family Pempheridae		
Pempheris ypsilychnus	M	*K. amamiensis*, *K. minithyrsites*
Order Atheriniformes		
Family Atherinidae		
Atherina hepsetus	M, B, Fr	*K. anatolica*, *K. stellula*
Order Batrachoidiformes		
Family Batrachoididae		
Batrachoides surinamensis	M, B	*K. viseuensis*
Order Beloniformes		
Family Belonidae		
Strongylura strongylura	M, B	*K. chilkaensis*
Family Exocoetidae		
Cypsilurus ago	M	*K. thyrsites*
Cypsilurus sp.	M	*K. thyrsites*
Family Hemiramphidae		
Hyporhamphus gamberur	M	*K. iwatai*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Beryciformes		
Family Berycidae		
Beryx splendens	M	*K. thyrsites*
Order Blenniiformes		
Family Blenniidae		
Parablennius gattorugine	M	*K. quadratum*
P. zvonimiri	M	*K. quadratum*
Order Callionymiformes		
Family Callionymidae		
Callionymus lyra	M	*K. quadratum*
Order Carangiformes		
Family Carangidae		
Alepes djedaba	M	*K. javaensis*, *K. pyramidalis*
Atropus atropus	M	*K. atropi*
Carangoides fulvoguttatus	M	*K. quadricornis*
C. plagiotaenia	M	*K. paraquadricornis*
Caranx crysos	M, B	*K. hypoepicardialis*
C. ignobilis	M, B	*K. paraquadricornis*
C. papuensis	M, B	*K. paraquadricornis*
C. sexfasciatus	M, B, Fr	*K. amamiensis*, *K. paraquadricornis*
Decapterus maruadsi	M	*K. decaptera*
D. russeli	M	*K. thyrsites*
Seriola dumerili	M	*K. amamiensis*, *K. insolita*
S. lalandi	M	*K. neurophila*, *K. thyrsites*
S. quinqueradiata	M	*K. amamiensis*, *K. iwatai*, *K. yasunagai*, *K. megacapsula*, *K. pericardialis*
Trachurus capensis	M	*K. nova*
T. mediterraneus	M, B	*K. quadratum*
T. picturatus	M	*K. nova*
T. trachurus	M	*K. azevedoi*, *K. nova*, *K. quadratum*, *K. thyrsites*
T. trecae	M	*K. nova*
T. japonicus	M	*K. trachuri*
Family Coryphaenidae		
Coryphaena hippurus	M, B	*K. thyrsites*
Family Istiophoridae		
Istiophorus platypterus	M	*K. musculoliquefaciens*
Family Xiphiidae		
Xiphias gladius	M	*K. musculoliquefaciens*
Order Centrarchiformes		
Family Latridae		
Latris lineata	M	*K. neurophila*
Family Oplegnathidae		
Oplegnathus fasciatus	M	*K. iwatai*, *K. yasunagai*
O. punctatus	M	*K. iwatai*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Cichliformes		
Family Cichlidae		
Aequidens plagiozonatus	Fr	*K. aequidens*
Chaetobranchopsis orbicularis	Fr	*K. orbicularis*
Order Clupeiformes		
Family Clupeidae		
Alosa aestivalis	M, B, Fr	*K. clupeidae*
A. mediocris	M, B, Fr	*K. clupeidae*
A. pseudoharengus	M, B, Fr	*K. clupeidae*
Brevoortia tyrannus	M, B	*K. clupeidae*
Clupea harengus	M, B	*K. clupeidae*
Konosirus punctatus	M, B	*K. guangdongensis*
Sardinella lemuru	M	*K. thyrsites*
Sardinops sagax	M	*K. thyrsites*
Family Engraulidae		
Engraulis australis	M, B	*K. thyrsites*
E. encrasicolus	M, B	*K. histolytica*
E. japonicus	M	*K. thyrsites*
Family Spratelloididae		
Spratelloides delicatulus	M	*K. thyrsites*
S. robustus	M, B	*K. thyrsites*
Order Cyprinodontiformes		
Family Fundulidae		
Fundulus heteroclitus	M, B, Fr	*K. funduli*
F. majalis	M, B	*K. funduli*
Order Gadiformes		
Family Gadidae		
Gadus chalcogrammus	M, B	*K. thyrsites*
Macruronus magellanicus	M	*K. alliaria*
Micromesistius australis	M	*K. alliaria*
M. poutassou	M	*K. thyrsites*
Pollachius pollachius	M	*K. thyrsites*
Family Merlucciidae		
Merluccius australis	M	*K. alliaria*
M. capensis	M	*K. thyrsites*
M. gayi	M	*K. hallado*, *K. peruvianus*
M. hubbsi	M	*K. alliaria*, *K. rosenbuschi*
M. productus	M, B	*K. paniformis*, *K. thyrsites*
Order Gobiiformes		
Family Butidae		
Kribia kribensis	Fr	*K. eleotrisi*
Family Gobiidae		
Acanthogobius hasta	M, B, Fr	*K. akihitoi*, *K. empressmichikoae*
Acentrogobius chlorostigmatoides	M, B, Fr	*K. acentrogobia*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Gobius cobitis	M, B	*K. nova*
G. cruentatus	M	*K. niluferi*
G. niger	M, B	*K. nova*
G. ophiocephalus	M, B	*K. nova*
Knipowitschia longicaudata	M, B, Fr	*K. nova*
Mesogobius batrachocephalus	M, B, Fr	*K. nova*
Neogobius melanostomus	M, B, Fr	*K. niluferi*, *K. nova*
N. fluviatilis	M, B, Fr	*K. nova*
Pomatoschistus microps	M, B, Fr	*K. camarguensis*, *K. nova*
P. minutus	M, B	*K. camarguensis*, *K. nova*
Ponticola cephalargoides	M	*K. nova*
P. eurycephalus	M, B	*K. nova*
P. platyrostris	M, B	*K. nova*
P. ratan	M, B	*K. nova*
P. syrman	M, B	*K. nova*
Proterorhinus marmoratus	M, B, Fr	*K. nova*
Tridentiger trigonocephalus	M, B, Fr	*K. nova*
Order Kurtiformes		
Family Apogonidae		
Cheilodipterus macrodon	M	*K. thalassomi*
Ch. quinquelineatus	M	*K. cheilodipteri*
Ostorhinchus aureus	M	*K. cheilodipteri*, *K. whippsi*, *K. iwatai*
O. cookii	M	*K. cookii*
O. cyanosoma	M	*K. cheilodipteri*, *K. whippsi*
O. doederleini	M	*K. whippsi*
O. fleurieu	M, B	*K. iwatai*
O. properuptus	M	*K. gunterae*, *K. whippsi*
Zoramia leptacantha	M	*K. leptacanthae*
Z. viridiventer	M	*K. leptacanthae*
Order Mugiliformes		
Family Mugilidae		
Chelon auratus	M, B, Fr	*K. dicentrarchi*, *K. trifolia*, *K. unicapsula*
Ch. labrosus	M, B, Fr	*K. dicentrarchi*
Ch. ramada	M, B, Fr	*K. dicentrarchi*, *K. trifolia*, *K. unicapsula*
Ch. saliens	M, B	*K. dicentrarchi*
Crenimugil crenilabis	M, B	*K. crenimugilis*
C. seheli	M, B, Fr	*K. dicentrarchi*
Ellochelon vaigiensis	M, B, Fr	*K. yasunagai*
Minimugil cascasia	Fr	*K. cascasia*
Mugil cephalus	M, B, Fr	*K. bora*, *K. dicentrarchi*, *K. tetraspora*, *K. intestinalis*, *K. iwatai*, *K. quadratum*, *K. surabayaensis*
M. japonica	M, B	*K. bora*
Osteomugil cunnesius	M, B, Fr	*K. borimiri*, *K. dicentrarchi*, *K. igori*, *K. valamugili*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
O. perusii	M, B	*K. bora*, *K. borimiri*, *K. dicentrarchi*, *K. fujitai*
Planiliza carinata	M, B	*K. bora*
P. melinoptera	M, B, Fr	*K. dicentrarchi*
P. parsia	M, B, Fr	*K. haridasae*, *K. sagarica*
Planiliza sp. D sensu	M, B, Fr	*K. borimiri*, *K. dicentrarchi*
Order Ophidiiformes		
Family Carapidae		
Echiodon sp.	?	*K. cutanea*
Order Perciformes		
Family Aulorhynchida		
Aulorhynchus flavidus	M	*K. thyrsites*
Family Cheilodactylidae		
Cheilodactylus zonatus	M	*K. whippsi*
Family Cottidae		
Icelinus filamentosus	M	*K. thyrsites*
Leptocottus armatus	M, B	*K. thyrsites*
Myoxocephalus brandtii	M	*K. nova*
M. scorpius	M, B	*K. quadratum*
Family Cyclopteridae		
Cyclopterus lumpus	M	*K. islandica*
Family Hexagrammidae		
Hexagrammos octogrammus	M	*K. azoni*
Ophiodon elongatus	M	*K. thyrsites*
Pleurogrammus azonus	M	*K. azoni*, *K. pleurogrammi*
P. monopterygius	M	*K. pleurogrammi*
Family Nototheniidae		
Patagonotothen canina	M	*K. alliaria*
P. ramsayi	M	*K. alliaria*, *K. ramsayi*
Family Pholidae		
Pholis ornata	M	*K. thyrsites*
Family Platycephalidae		
Platycephalus sp.	?	*K. iwatai*
Family Polynemidae		
Pentanemus quinquarius	M, B	*K. iidae*
Family Sebastidae		
Sebastes elongatus	M	*K. miniauriculata*
S. minor	M	*K. sebastea*
S. paucispinis	M	*K. clupeidae*, *K. miniauriculata*
Family Serranida		
Cephalopholis boenak	M	*K. thalassomi*
Hyporthodus nigritus	M	*K. hypoepicardialis*
Morone saxatilis	M, B, Fr	*K. cerebralis*
Family Zoarcidae		
Zoarces americanus	M, B	*K. clupeidae*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Pleuronectiformes		
Family Bothidae		
Arnoglossus imperialis	M	*K. lunata*
A. laterna	M	*K. lunata*
A. thori	M	*K. lunata*
Family Cynoglossidae		
Cynoglossus senegalensis	M, B, Fr	*K. cynoglossi*
Family Paralichthyidae		
Paralichthys adspersus	M	*K. thyrsites*
P. olivaceus	M	*K. lateolabracis*, *K. paralichthys*, *K. septempunctata*, *K. shiomitsui*, *K. thyrsites*, *K. yasunagai*
Family Pleuronectidae		
Atheresthes stomias	M	*K. aburakarei*, *K. thyrsites*
Hippoglossus stenolepis	M	*K. thyrsites*
Lepidopsetta bilineata	M	*K. thyrsites*
Microstomus pacificus	M	*K. thyrsites*
Parophrys vetulus	M	*K. thyrsites*
Platichthys flesus	M, B, Fr	*K. clupeidae*
Family Scophthalmidae		
Zeugopterus punctatus	M	*K. kabatai*
Order Salmoniformes		
Family Salmonidae		
Oncorhynchus gorbuscha	M, B, Fr	*K. thyrsites*
O. kisutch	M, B, Fr	*K. thyrsites*
O. mykiss	M, B, Fr	*K. thyrsites*
O. tshawytscha	M, B, Fr	*K. thyrsites*
Salmo salar	M, B, Fr	*K. thyrsites*
Order Scombriformes		
Family Centrolophidae		
Hyperoglyphe japonica	M	*K. ogawai*
Icichthys australis	M	*K. vesica*
Family Gempylidae		
Thyrsites atun	M, B	*K. thyrsites*
Family Nomeidae		
Nomeus gronovii	M	*K. hypoepicardialis*
Family Pomatomidae		
Pomatomus saltatrix	M, B	*K. clupeidae*, *K. hypoepicardialis*, *K. nova*
Family Scombridae		
Auxis thazard	M	*K. histolytica*
Euthynnus alletteratus	M, B	*K. nova*
Grammatorcynus bicarinatus	M	*K. grammatorcyni*
Rastrelliger kanagurta	M	*K. quraishii*, *K. saudiensis*
Sarda sarda	M, B	*K. histolytica*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Scomber japonicus	M	*K. caudata*, *K. histolytica*, *K. scomberi*, *K. thyrsites*
S. scombrus	M, B	*K. histolytica*, *K. thyrsites*
Scomberomorus commerson	M	*K. crumena*, *K. permulticapsula*, *K. scomberomori*
S. maculatus	M	*K. crumena*
S. niphonius	M	*K. konishiae*
S. sierra	M	*K. rayformis*
Thunnus albacares	M, B	*K. crumena*, *K. hexapunctata*, *K. neothunni*
T. alalunga	M	*K. thunni*
T. obesus	M	*K. nova*
T. orientalis	M, B	*K. hexapunctata*, *K. prunusi*, *K. yasunagai*
T. thynnus	M, B	*K. clupeidae*, *K. nova*
Family Trichiuridae		
Lepidopus caudatus	M	*K. thyrsites*
Trichiurus lepturus	M, B	*K. mirabilis*
Order Scorpaeniformes		
Family Anarhichadidae		
Anarhichas lupus	M	*K. islandica*
A. minor	M	*K. islandica*
Order Siluriformes		
Family Ariidae		
Ariopsis felis	M, B	*K. shkae*
Plicofollis layardi	M, B	*K. tachysurae*
P. platystomus	M, B	*K. bengalensis*
P. polystaphylodon	M, B, Fr	*K. quadratum*
Family Plotosidae		
Plotosus lineatus	M, B	*K. yasunagai*
Order Syngnathiformes		
Family Syngnathidae		
Entelurus aequoreus	M, B	*K. quadratum*
Syngnathus abaster	M, B, Fr	*K. quadratum*
S. acus	M, B	*K. quadratum*
S. tenuirostris	M	*K. quadratum*
Order Tetraodontiformes		
Family Tetraodontidae		
Sphoeroides annulatus	M, B	*K. dianae*
Takifugu rubripes	M, B, Fr	*K. shiomitsui*, *K. yasunagai*
Order Zeiformes		
Family Zeidae		
Zeus capensis	M	*K. thyrsites*
Z. faber	M, B	*K. thyrsites*

Note: *, all systematic groups and species are alphabetized, starting from cartilaginous fishes and ending with bony fishes; **, habitation in waters of different salinity (M, marine water; B, brackish water; Fr, freshwater environment).

Given the hypothesis that myxosporeans originated from marine fish [Shulman et al., 1997] and considering the overwhelming prevalence of *Kudoa* findings in saline water basins, it can be concluded as follows: the transition to parasitizing in some freshwater hosts occurred evolutionally later and likely involved euryhaline hosts.

Also, seven *Kudoa* species have been documented in marine fish inhabiting estuarine zones. In particular, they were found in euryhaline mullets. Thus, *Kudoa haridasae* Sarkar & Ghosh, 1991 and *Kudoa sagarica* Das, 1996 were reported from the goldspot mullet *Planiliza parsia* (Hamilton, 1822) (the Indian Ocean, the Hooghly estuary, Western Bengal, India) [Das, 1996; Sarkar, Chaudhury, 1996]. *K. unicapsula* was registered in the thinlip mullet *Chelon ramada* (Risso, 1827) and golden grey mullet *Ch. auratus* (Risso, 1810) (the Mediterranean Sea, Santa Pola, Ebro River delta, Spain) [Yurakhno et al., 2007]. Besides, myxosporeans were found in brackish-water gobies: *Kudoa camarguensis* Pampoulie, Marques, Rosecchi, Crivelli & Bouchereau, 1999 was recorded from the sand goby *Pomatoschistus minutus* (Pallas, 1770) and common goby *P. microps* (Krøyer, 1838) (the Mediterranean Sea, Rhône River delta, France) [Pampoulie et al., 1999]. *Kudoa cerebralis* Paperna & Zwerner, 1974 was noted in the striped bass *Roccus saxatilis* (Walbaum, 1792) from the Atlantic Ocean, where this species chiefly occurs in estuaries (North American Coast, mouths of Rappahannock and York rivers) and occasionally in marine waters (the Chesapeake Bay coast, the USA) [Paperna, Zwerner, 1974]. This host species is anadromous, migrating between freshwater and marine basins. Its spawning commonly occurs in freshwater. *K. inornata* was found in an estuarine fish, *Cynoscion nebulosus* (Cuvier, 1830) (the Atlantic Ocean, South Carolina coast, the USA, Romaine Harbor, Ashley River, Ashepoo, Combahee, and Edisto basin) [Dykova et al., 2009]. *Kudoa viseuensis* Monteiro, Da Silva, Hamoy, Sanches & Matos, 2019 was noted in a marine host, *Batrachoides surinamensis* (Bloch & Schneider, 1801), near the spot of the Amazon River inflow into the Atlantic Ocean (Viseu municipality, state of Pará, northern Brazil) [Monteiro et al., 2019]. Another *Kudoa* sp. was reported from a brackish-water host, the white perch *Morone americana* (Gmelin, 1789), in the Atlantic Ocean basin, in the Choptank River, Chesapeake Bay (Maryland, the USA) [Bunton, Poynton, 1991].

Only one ocean myxosporean species, *K. thyrsites*, is known to infect five anadromous salmonids: four Pacific species [the pink salmon *Oncorhynchus gorbuscha* (Walbaum, 1792), coho salmon *O. kisutch* (Walbaum, 1792), rainbow trout *O. mykiss* (Walbaum, 1792), and Chinook salmon *O. tshawytscha* (Walbaum, 1792)] and one inhabitant of the Atlantic and Arctic oceans [the Atlantic salmon *Salmo salar* Linnaeus, 1758] [Eiras et al., 2014]. This evidences for the likelihood that host infestation by this parasite occurs exclusively in marine habitats.

Thus, out of 128 *Kudoa* species, 117 (91.4%) were found in marine zones of the World Ocean, 8 (6.3%) were recorded in its estuaries (7 species in marine fish, and 1 in a freshwater host), and 3 (2.3%) were registered in freshwater bodies.

To assess the effect of desalination on myxosporean fauna in fish of the Black Sea and Sea of Azov, we conducted long-term studies in Crimean estuarine ecosystems focusing, among other issues, on *Kudoa* in gobies. In 2008–2019, we examined myxosporeans in 308 gobies in the Chernaya River mouth, 807 specimens in the Karkinitsky Bay (the Black Sea), and 757 Gobiidae specimens in Eastern Sivash (the Sea of Azov) (Table 2).

Table 2. Number of fish infected with *Kudoa nova* / number of fish studied (average prevalence, %) of the family Gobiidae, with indication of hosts prevalence in areas of various water salinity

Area	The Black Sea				The Sea of Azov						The Bug River	Narew and Vistula rivers
	The Chernaya River mouth	The Karkinitsky Bay		The Dnieper River mouth	Eastern Sivash					The Tagan-rog Bay		
					Northern area	Central area		Southern, inner area				
Research period	2010–2019	2008–2013	2014–2017	2012	2010, 2013	2010, 2013	2014–2016	2013	2014–2015	1998	2011	2011
Water salinity, ‰	12–16 (at the bottom)	10–15	18.6–27.6	0.05–16	1–11.5	10–40	22.7–65	10–40	22.7–75	1–3	0.25–0.5	0.2–0.573
Fish species												
Gobius niger	2 / 17 (11.8)	–	–	–	–	–	–	–	–	–	–	–
G. ophiocephalus	4 / 82 (4.9)	0 / 61 (0)	0 / 209 (0)	–	0 / 105 (0)	0 / 30 (0)	0 / 58 (0)	–	0 / 3	–	–	–
Mesogobius batrachocephalus	–	–	0 / 2	–	–	–	–	0 / 1	–	–	–	–
Neogobius fluviatilis	–	13 / 35 (37.1)	35 / 98 (35.8)	–	1 / 7	–	12 / 16 (75)	–	4 / 18 (22.2)	0 / 14 (0)	0 / 24 (0)	0 / 118 (0)
N. gymnotrachelus	–	–	–	–	–	–	–	–	–	–	0 / 35 (0)	0 / 85 (0)
N. melanostomus	40 / 79 (50.6)	27 / 80 (33.8)	48 / 271 (17.7)	1 / 37 (2.7)	11 / 74 (14.9)	–	53 / 127 (41.7)	54 / 230 (23.5)	41 / 88 (46.6)	0 / 2	–	0 / 21 (0)
Pomatoschistus microps	–	–	0 / 3	–	–	–	–	–	–	–	–	–
Ponticola eurycephalus	13 / 75 (17.3)	–	–	–	–	–	–	–	–	–	–	–
Proterorhinus marmoratus	22 / 43 (51.2)	–	28 / 48 (58.3)	–	–	–	–	–	–	–	–	–
P. semilunaris	–	–	–	–	–	–	–	–	–	–	–	0 / 24 (0)
Tridentiger trigonocephalus	2 / 12 (16.7)	–	–	–	–	–	–	–	–	–	–	–
Fish in total, ind.	308	176	631	37	186	30	201	231	109	16	59	248

We analyzed species composition and abundance of fish parasites in two estuarine biotopes in the area of the Chernaya River inflow to the Sevastopol Bay (the Black Sea): in the river mouth with increased bottom salinity and in 1,5 km upstream, in a biotope with salinity of 4–5‰ [Yurakhno, 2012, 2014, 2015a]. In investigated hydrobionts, along with eight predominantly marine myxosporeans, one *Kudoa* representative – *K. nova* – was found from the chameleon goby *Tridentiger trigonocephalus* (Gill, 1859), grass goby *Gobius ophiocephalus* Pallas, 1814, black goby *G. niger* Linnaeus, 1758, tubenose goby *Proterorhinus marmoratus* (Pallas, 1814), mushroom goby *Neogobius eurycephalus* (Kessler, 1874), and round goby *N. melanostomus* (Pallas, 1814). Infestation prevalence by this parasite varied 5 to 92% for different hosts in different seasons. In our study, *K. nova* was noted in a biotope with bottom salinity of 12–16‰. This species was absent in freshwater area of the Chernaya River we surveyed owing to the lack of hosts (gobies) in catches.

K. nova was analyzed in gobies of the Karkinitsky Bay in 2008–2018. It was recorded in three gobies: in the round goby, monkey goby *Neogobius fluviatilis* (Pallas, 1814), and tubenose goby, while the grass goby and knout goby *Mesogobius batrachocephalus* (Pallas, 1814) were free of this parasite. Fish were caught from areas with various hydrological conditions. Some sampling sites were located 8–13 km from our base, the Portovoye village (the Andreevka, Avrora, Steregushchee, and Risovoe villages). Thus, in 2008–2013, gobies were sampled in open sea zones periodically affected by freshwater inflow from paddy fields near the Portovoye and Risovoe and in more distant spots near the Avrora and Steregushchee. In different seasons, prevalence of *K. nova* infestation in the monkey goby from slightly desalinated zones was significantly high (31–56%). Infestation rates in the round goby were also high and comparable across different salinity gradients (40–47%), except for the site in the Risovoe vicinity, where it was only 12%. In subsequent years, after rice cultivation ceased in the Crimea, *K. nova* persisted in gobies, with infestation prevalence dropping noticeably in the round goby (down to 4–30%), but remaining sometimes rather elevated in the monkey goby (up to 47–63%).

In 2014 and 2015, fish was sampled near the former Andreevka village (opposite the Ogni settlement) and in the Avrora southward to the Portovoye, closer to the Bakalskaya Spit. Sampling depth was slightly more than 1 m; interestingly, by fishermen evidences, such depths stretch only along 200 m from the coast and are characterized by sandy substrates (clay-mixed sediments in the Avrora vicinity). Here, only 10% of the round goby individuals were infected with *K. nova*. In 2014, the monkey goby was sampled once from a shallow brackish lagoon (salinity of 27.60‰) in the Portovoye vicinity, on the Sary-Bulat Spit, with silty substrate; 18% of fish were infected with *K. nova*. The highest infestation rates of gobies by this parasite were recorded in 2015 in a shallow Sary-Bulat Lagoon near the Portovoye. There, depths of 10–60 cm extend over 2 km toward islands, and bottom is a black silt. Salinity gradients differed as well: areas near the Andreevka and Avrora experienced minimal freshwater effect, while shallow waters in the Portovoye vicinity were affected by six Dnieper River discharge channels until 2014. Subsequent data obtained for the open sea and adjacent Sary-Bulat Lagoon confirmed higher infection rates in the lagoon. For example, prevalence of *K. nova* infestation in the round goby from the Sary-Bulat Lagoon was 4 times higher in 2016 and 2.6 times higher in 2017 than in fish from the open sea. The monkey goby in the lagoon showed the prevalence of 63%, and the tubenose goby, 50–65%. Accordingly, higher infection rates of fish with myxosporeans were recorded in shallower and highly silty areas of the Karkinitsky Bay that seems to reflect intensified accumulation of infective stages there [Dmitrieva et al., 2015; Korniichuk et al., 2016; Yurakhno, 2013, 2015a, 2016b; Yurakhno, Tokarev, 2017].

In general, in the Swan Islands nature reserve, *Kudoa* representatives and other myxosporeans form a typical marine fauna, and it is consistent with salinity dynamics in the area. According to data provided by N. Shadrin (IBSS), salinity in periodically desalinated open sea in the Risovoe and Portovoye vicinity fluctuated between 10 and 15‰ within 2008–2013. After the cessation of freshwater discharge from paddy fields, salinity near Portovoye increased. In the open sea, we recorded the values of 19.30‰ in 2014, 21.08‰ in 2015, and 17.90–18.59‰ in 2016. In the Sary-Bulat Lagoon, salinity reached 20.87‰ in 2015 and 18.14–21.35‰ in 2016. Apparently, periodic freshwater inflow from paddy fields into the Karkinitsky Bay did not reduce salinity to levels critical for *K. nova* survival, unlike in other areas analyzed (see below).

Another estuarine biotope we examined for *Kudoa* was Eastern Sivash. The round, grass, and monkey gobies were sampled in November–December 2010 in its northern area, near the Mysovoe, Chaikino, and Chongar villages [Yurakhno, 2015a; Yurakhno, Gorchanok, 2011]. Fish were sampled with fixed nets at depths of 2–4 m; water temperature was of +10…+14 °C; and areas were characterized by various salinity. In the Mysovoe and Chaikino vicinity, salinity during sampling was 11.5‰. As known according to data provided by A. Boltachev (IBSS), the value could drop down to 1‰ due to occasional freshwater discharge from paddy fields to Sivash. In the Chongar vicinity, salinity was 17‰. In 2010, *K. nova* was absent in 47 round gobies sampled from desalinated zones of the Mysovoe and Chaikino, but it was registered in 1 out of 5 monkey gobies. In the Chongar area, 43% of round gobies were infected, and there were no *K. nova* in 1 monkey goby caught. In 2013, prevalence in the round goby near Mysovoe rose to 47% suggesting the lack of strong freshwater effect in this spot in previous years.

From December 2012 to June 2015, we carried out further studies on myxosporeans in gobies in Eastern Sivash, with the focus on its hypersaline inner zone (the Semisotka and Kamenskoe villages) and central area (the Dmitrovka village). The round, sand, grass, and knout gobies were surveyed [Yurakhno, 2015a]. One species of parasite – *K. nova* – was registered in muscles of the round and sand gobies.

Infestation prevalence of examined fish varied seasonally and annually: it was 22% in the monkey goby and 16–69% in the round goby. Neither inner zone of Eastern Sivash, nor its central area was highly desalinated; values of host infestation by *K. nova* were rather noticeable and comparable to those in marine waters, the same as in 2013 in the northern lagoon. This fact was proved by data of other researchers [Shadrin et al., 2018]. Thus, in 2013, water salinity in the central and inner areas varied within 10.0–40.0‰ (mean of 25.2‰). In 2014, it was 25.9–26.7‰ in summer and 22.7–42.2‰ in autumn; at several spots, salinity reached 50.0–65.0‰. In 2015, it was 55.0–65.0‰ in the central area and 70.0–75.0‰ in the southern one.

The cessation of freshwater inflow from paddy fields in 2014 to Eastern Sivash likely improved conditions for *K. nova* proliferation in local populations of gobies. This is evidenced by higher infection rates in the round goby (up to 53–69% in various seasons) in recent years of the study in the hypersaline inner zone of Sivash – in the Kamenskoe vicinity. It is the southernmost area, the furthest from paddy fields, and the one with maximum salinity [Yurakhno, 2015a].

K. nova was a common species in the parasite fauna of gobies for all three estuarine ecosystems surveyed.

Our data for periodically desalinated marine areas in the Crimea evidence for a negative effect of strong desalination (down to 1‰ or lower values) on infection rates of gobies by *K. nova*. Conversely, higher infection rates were observed in areas with elevated salinity (Table 2). When analyzing changes in mean infestation prevalence by this parasite in gobies up to 2013 (a period of discharge from paddy fields into the Karkinitsky Bay and Sivash, including designated spots within the latter one) and in later periods, we observed shifts in the round goby alone. Interestingly, these changes are contradictory between the areas compared. Thus, since 2014, mean infestation prevalence of the goby by *K. nova* in the Karkinitsky Bay decreased by nearly twofold, whereas in the inner Sivash zone, it doubled. This suggests that factors other than salinity may affect these dynamics.

The absence or sporadic occurrence of *K. nova* in highly desalinated areas of the Ponto–Azov region is corroborated by both literature data and our own information. According to N. Naidenova [1974] and our expeditionary research, this parasite was absent in summer 1998 in gobies sampled in the highly desalinated Taganrog Bay (the Sea of Azov) into which the Don River flows [Yurakhno, Gorchanok, 2011]. According to data of AzNIIRKh researches, the mean salinity in the area was 1–3‰. Similarly, during summer 2011, no myxosporeans were noted in the parasite fauna of invasive gobies that spread from the northwestern Black Sea along the central invasive corridor: the round goby *N. melanostomus*, racer goby *N. gymnotrachelus* (Kessler, 1857), monkey goby *N. fluviatilis*, and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837). These fish were sampled in the Bug and Vistula rivers. In 2012, the prevalence of *K. nova* infestation in the Dnieper River estuarine zone, near Ochakiv city, was only 2.7% [Kvach et al., 2014] (Table 2).

A near-complete absence of this species or its significantly low occurrence in hosts from highly desalinated areas evidence for the following. The first, *K. nova* spores which spend most time after the host death in the water column, in sediment, or substrate may not survive low salinity. The second, the species composition of oligochaetes and polychaetes – potential definitive hosts for myxosporeans – is notably scarce in regions with the pronounced desalination and salinity fluctuations. However, a two-host life cycle of myxosporeans has only been confirmed for 36 out of more than 2,000 species [Dykova, Lom, 2007]. Most of them are freshwater inhabitants, and none of them belong to the genus *Kudoa*. Thus, we just hypothesize that not only fish, but also invertebrates may participate in *K. nova* life cycle.

To assess spore survival under different salinities, an experiment was carried out in summer 2014 [Yurakhno, 2015b, 2016a, 2018]. Cysts isolated from host muscle tissue were stored in spring water (freshwater) in refrigerator. After 3 days, nearly half of spores in freshwater featured structural abnormalities, including deformities. By the 34th day, 87% of spores in freshwater were degraded, and the function of the polar filament extrusion was disrupted in alkaline solutions indicating loss of viability of darkened spores. In contrast, the most comfortable conditions were formed in cysts immersed in seawater in refrigerator; there, the share of normal spores was 94–98% throughout month-long experiments. As for cysts in muscles, the key role in spore preservation was played by their occurrence in host tissues in biochemical environment. In this case, shares of abnormal spores in freshwater and marine water at ambient temperature were comparable and relatively low: in freshwater, 9 to 17%, and in seawater, 4 to 20%.

The rapid detrimental effect of freshwater on *K. nova* spores is surprising given their presumed resilience and theoretical ability to persist longer in unsuitable environment. This parasite is known to tolerate slight desalination; it occurs in significantly higher abundance in mesohaline shallows of the Sea of Azov than in the Black Sea, especially in estuaries. However, pure freshwater directly disrupts structure and viability of these spores when exposed to unsuitable environment. When *K. nova* spores remain within muscle tissue of the host, its biochemical environment mitigates adverse effects of freshwater. In contrast, spores of oceanic species are often more affected by freshwater, and this effect can be detrimental. Thus, a proven method to inactivate spores of *K. septempunctata* – a parasite causing diarrhea and vomiting in consumers of raw meat of *Paralichthys olivaceus* (Temminck & Schlegel, 1846) – is to immerse it in freshwater (0‰) or a hypersaline solution (160‰) for five minutes [Yokoyama et al., 2016].

We registered *K. nova* in both fully saline Black Sea waters and mesohaline Sea of Azov ones (there, infestation prevalence often reached 100% in host fish inhabiting shallow estuaries). However, we recorded no specimens of this parasite in oligohaline and freshwater habitats. *K. nova* spores exhibit negative buoyancy, and this is regarded as an adaptation for infecting benthic hosts. In lower-salinity environments, spores settle more rapidly onto a substrate mixing with surface silt layer and thereby optimizing the contact with potential hosts. *K. nova* proliferation into oligohaline and freshwater systems seems to reflect the limited occurrence of its putative definitive hosts: in these habitats, possibly oligochaetes or polychaetes. Moreover, as demonstrated by our experiments, *K. nova* spores cannot survive prolonged exposure to freshwater after the host death. Accordingly, this parasite is likely of marine origin; it occurs in water basins of various salinity (including oceanic one) and is widely distributed in Gobiidae representatives in the Black Sea and Sea of Azov [Yurakhno, 2014; Yurakhno, Gorchanok, 2011].

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ВЛИЯНИЕ ФАКТОРА СОЛЁНОСТИ ВОДЫ НА РАСПРОСТРАНЕНИЕ МИКСОСПОРИДИЙ РОДА *KUDOA* (CNIDARIA, MYXOZOA) СРЕДИ РЫБ МИРОВОЙ ФАУНЫ

В. М. Юрахно

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Изучена встречаемость миксоспоридий рода *Kudoa* в рыбах, обитающих в водах разной солёности. Работа основана на собственных материалах по миксоспоридиям рыб, собранных в 1987–2021 гг. Это более чем 12 000 экз. около 100 видов рыб в бассейнах Атлантического океана [Азовское (Россия, Украина), Чёрное (Россия, Украина, Турция) и Средиземное (Италия, Испания) моря; регионы Центрально-Восточной Атлантики (на траверзе Мавритании) и южные широты у берегов Африки (на траверзе Намибии); вóды северной (недалеко от Норвегии) и южной (на траверзе Аргентины) частей океана; юго-восточные берега США], Индийского океана [побережье Йемена] и Тихого океана [Южно-Китайское море (Вьетнам)]. Всего на оригинальном материале исследовано 27 представителей миксоспоридий рода *Kudoa*, из которых 19 определены до вида. Также проанализированы все доступные литературные источники и электронная база FishBase. Установлено, что из 291 представителя рыб — хозяев *Kudoa* 169 видов являются чисто морскими, 76 видов могут обитать в морской и солоноватоводной среде, 42 вида эвригалинны и могут быть встречены как в морских и солоноватых, так и в пресных водах, и лишь 4 вида являются чисто пресноводными. Из 128 видов *Kudoa* 117 (91,4 %) были найдены в морской зоне Мирового океана, 8 (6,3 %) — в его эстуариях (7 видов — в морских рыбах, 1 вид — в пресноводном хозяине), 3 (2,3 %) — в пресноводных водоёмах. В 2008–2019 гг. проведены исследования *Kudoa nova* Naidenova, 1975 в экосистемах эстуарного типа у берегов Крыма в устье реки Чёрная и в Каркинитском заливе (Чёрное море), а также в Восточном Сиваше (Азовское море). Всего вскрыто 2232 экз. 11 видов бычковых рыб. Установлено, что периодическое опреснение этих районов водами рисовых чеков, а также постоянное присутствие пресной воды в поверхностном слое устья реки Чёрная не вызывали сильного изменения солёности (за исключением мелководной северной части Восточного Сиваша), которое было бы губительным для данного вида паразитов. При этом *K. nova* полностью отсутствовала в бычках, выловленных в 1998 г. в значительно опреснённом водами реки Дон Таганрогском заливе Азовского моря. Не обнаружена она и в 2011 г. в реках Буг и Висла при исследовании микропаразитов бычков, распространившихся из северо-западной части Чёрного моря по центральному инвазивному коридору. Поставленный нами опыт засвидетельствовал негативное влияние пресной воды на споры данного паразита: под её воздействием они деформировались и темнели; также нарушалась функция выстреливания полярной нити.

Ключевые слова: миксоспоридии, *Kudoa*, солёность воды, мировая фауна

1871
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Морской биологический журнал
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CHRONICLE AND INFORMATION

ON THE ANNIVERSARY OF D. SC., PROF. IGOR DOVGAL

On 29 October, 2024, D. Sc., Prof. Igor Dovgal celebrated his 70th birthday. He is a renowned protistologist heading the laboratory of population biology of hydrobionts at the A. O. Kovalevsky Institute of Biology of the Southern Seas of the Russian Academy of Sciences.

I. Dovgal was born on the Sakhalin Island into a military family. In 1959, he moved to Kyiv with his parents. In 1980, he graduated from the faculty of biology of the Taras Shevchenko Kyiv State University specializing in zoology and botany. While still a student, he began studying parasitic ciliates in the laboratory of invertebrates at the I. I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine and successfully defended his coursework and diploma thesis. He joined the Institute of Zoology in 1979 and worked there until 2014.

A young protistologist was interested in poorly studied groups of infusoria: suctorians and chonotrichs. In 1981–1982, he completed a one-year internship at the Zoological Institute of the Academy of Sciences of the Soviet Union in Leningrad under the guidance of D. Sc. A. Yankovsky, a well-known specialist on infusoria.

In 1989, Igor Dovgal defended his PhD thesis in Kyiv, “Tentaculate Infusoria (Ciliophora, Suctoria) of the Ukrainian Polesia.” In 2003, he defended his D. Sc. dissertation in Saint Petersburg, “Evolution, Phylogeny, and Systematics of Tentaculate Infusoria (Ciliophora, Suctorea).”

Within 1987–1992, he was involved in studying the ecological consequences of the Chernobyl disaster.

In 2005, the Higher Attestation Commission of Ukraine awarded I. Dovgal the scientific title of senior researcher. In 2010, by decree of the Minister of Education and Science of Ukraine, he was awarded the title of Professor.

Over the years of his professional activity, Igor Dovgal contributed much to the development of protistology as a systematist. As a result of his systematic and nomenclatural revisions, he substantiated the identification of 1 order, 1 suborder, and 4 families of infusoria and described 6 new genera and 23 new species.

He developed an original concept of the hydrodynamic boundary water layer as an adaptive zone for sessile protozoans, a von Baer’s law for unicellular eukaryotes (“the principle of tomite similarity”), and a hypothetical evolutionary scenario for the formation of morphogenetic mechanisms during the transition of unicellular eukaryotes to multicellularity. Together with co-authors, he proposed a scale-dependent model for distribution of marine planktonic infusoria. In collaboration with researchers from Switzerland and China, he developed a phylogenetic scheme for ciliates of the subclass Chonotrichia. This scheme is based on comparative morphology, ontogeny, and molecular genetics.

I. Dovgal has published over 250 scientific works, including 4 monographs, 138 articles (55 in Web of Science indexed journals and 20 in Scopus indexed ones), 1 popular science book, and 4 biology textbooks. He became the editor-in-chief of the Red Data Book of Sevastopol. Moreover, he is a co-author of two invention patents in Ukraine.

In 2004–2014, Igor Dovgal headed the department of fauna and invertebrate systematics, and in 2007–2014, he was the deputy director for scientific affairs at the I. I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine. In 2003–2013, he taught at Zhytomyr State University.

Since 2016, I. Dovgal is a chief researcher at IBSS, member of the Institute's dissertation council, and deputy chairman of the scientific council.

He serves on editorial boards of five scientific journals: Biodiversity and Sustainable Development, Ecologica Montenegrina, Ecosystems, Marine Biological Journal, and Protistology. Also, he is a member of the topical advisory panel of the scientific journal Diversity. Igor Dovgal joined the International Society of Protistologists (ISOP) in 2006, served as its Vice President in 2007–2008, and became its Emeritus Member in 2022. Since 2021, he is a member of the Russian Hydrobiological Society.

For many years, I. Dovgal carried out joint research with foreign colleagues, participated in international scientific meetings at institutions in Germany, Denmark, Turkey, Montenegro, Italy, and Mexico, and lectured at Shandong University (SDU) and National Autonomous University of Mexico (Universidad Nacional Autónoma de México, UNAM). His co-authors represent 30 countries. Igor Dovgal actively participates in expeditionary research, conferences, congresses, and symposia.

He lectures "Systematics and Morphology of Hydrobionts" and "Population Biology of Hydrobionts" for master students of the department of hydrobiology and general ecology at the Sevastopol State University. He has supervised ten PhDs and one D. Sc.

For his significant contribution to science and outstanding achievements, I. Dovgal has been awarded the I. I. Schmalhausen Prize of the National Academy of Sciences of Ukraine. He received a letter of gratitude from the Governor of Sevastopol, a letter of gratitude from the Department of Natural Resources and Ecology of Sevastopol, and a certificate of honor from the Russian Academy of Sciences.

Friends and IBSS colleagues warmly congratulate Igor Dovgal on his anniversary and wish him good health and fruitful work for the benefit of national and global science.

Dear Igor Vasilyevich, in you, our institute has gained a highly skilled specialist, a talented teacher, a kind-hearted colleague, and an honest and decent person, and we all have found a true friend!

К ЮБИЛЕЮ ДОКТОРА БИОЛОГИЧЕСКИХ НАУК, ПРОФЕССОРА ИГОРЯ ВАСИЛЬЕВИЧА ДОВГАЛЯ

29 октября 2024 г. своё 70-летие отметил д. б. н., проф. Игорь Васильевич Довгаль, заведующий лабораторией популяционной биологии гидробионтов ФИЦ ИнБЮМ. Известный протистолог И. В. Довгаль — автор и соавтор более чем 250 научных работ и один из ответственных редакторов Красной книги города Севастополя. Также Игорь Васильевич входит в состав редколлегий пяти научных журналов.

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TRIBUTE TO A WONDERFUL PERSON AND ICHTHYOLOGIST, LIDIYA OVEN

© 2025 **T. Bagnyukova[1] and A. Pashkov[2]**

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accepted for publication 25.12.2024.

Lidiya Oven, a remarkable person and brilliant ichthyologist, passed away in January 2021. She contributed much to ichthyology, especially to investigation of fish reproductive biology, by building and developing the methodological principles for studying oogenesis and reproduction of portion-spawning marine fish. Her human and personal qualities are no less important to us. We, her former graduate students, would like to honor her memory with this informal obituary. We both were graduate students in difficult times: in the early 1990s, when a decision to become a scientist was not trivial in itself. Lidiya Oven supervised our first steps in science and taught us to analyze the biological processes on our own; her contribution to the shaping us as researchers was invaluable. With this publication, we would like to remind about this wonderful person to new generations of young biologists.

> Perhaps it is true that nothing worth knowing can be taught–
> all the teacher can do is [to] show that there are paths.
>
> *Richard Aldington, 1933*

Lidiya Oven (nee Egurazdova) was born on 6 May 1930 in Pervomaysky village in the Gorky region (today, Nizhnegorodsky region). Her father was a CPSU (Communist Party of the Soviet Union) representative and trade union steward, while her mother was a homemaker, who raised five children.

In 1953, L. Oven defended her diploma thesis, *Migration of embryos and larvae of pelagophilic fishes in the Amur River near Yelabuga in the summer of 1952*, and graduated Lomonosov Moscow State University (MSU) with a specialist degree in zoology–ichthyology from the Department of Ichthyology in the Faculty of Biology and Soil Science, thus launching her long scientific career studying the reproductive biology of fish.

There are ten graduates from the Department of Ichthyology in 1953 listed on the MSU website (http://ichthyology.msu.ru/?page_id=84): Yuriy Yurovitskiy, I. Vasil'yeva, D. Arrojo Bueno, Al'vina Matveeva, Boris Vronsky, V. Mityushkin, Petr Borogoditsky, **Lidiya Egurazdova (Oven)**, Elza Pompik (Kalinina), and Juanita Montes Kanad.

After working for nearly a year in her native department of ichthyology at MSU, L. Oven moved to the Crimea in 1954 [To the memory of Lidiya Oven, 2021] and started her work at the Karadag Biological Station. Today, it is formally known as the T. I. Vyazemsky Karadag Scientific Station;

it is a nature reserve of the Russian Academy of Sciences (RAS) and branch of the A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS (IBSS).

After the Second World War, the Karadag Biological Station became known for its marine research in the Soviet Union. Konstantin Vinogradov, an outstanding marine biologist and ichthyologist, had been its director until 1952, devoting much effort to developing numerous research fields, training students, and bolstering scientific educational activity in this beautiful corner of the Crimea.

The 1960s, the Karadag Biological Station laboratory building (left) and administrative building (right) with a library and first-aid post. Above at a distance stands the hydrometeorological station where its staff lived. Source: personal archive of N. Kustenko

Remembering K. Vinogradov, his son wrote that in the postwar years, Karadag was a prominent marine research center in the USSR. Many world-renowned scientists came here during that period: biochemist A. Palladin; biologists Academicians E. Pavlovsky, E. Kreps, L. Zenkevich, B. Bykhovsky, and G. Gauze; Corresponding Member of the Academy of Sciences of the Soviet Union P. Svetlov; Professors A. Lyubishchev and N. Gaevskaya; geologists Academicians D. Shcherbakov and Corresponding Member M. Muratov; astronomer Academician V. Fesenko, *etc.* Exchanging ideas with them was an excellent learning opportunity for Konstantin Vinogradov and other researchers at the Station. Scientific seminars and meetings were often held here, and tens of students, biologists, geographers, and geologists, as well as all manner of famous university teachers, visited the Karadag Biological Station every year [Vinogradov, 2009].

The Karadag old-timers recalled that the research community at the Station was a hotbed for innovation in the 1950–1960s. A powerhouse scientific collective had formed here and was studying marine and terrestrial ecosystems of the Crimea with great enthusiasm. The staff was regularly replenished with young specialists. This was the environment in which Lidiya Oven found herself in 1954. First as a junior researcher (1954–1959) and then as acting scientific secretary (1960–1963), she studied reproductive characteristics of Black Sea fishes, primarily their oogenesis and fertility.

In 1950, K. Vinogradov and K. Tkacheva had found and described multi-portion spawning in fish inhabiting the Black Sea [Vinogradov, Tkacheva, 1950], but it was L. Oven who studied in detail the multi-portion spawning and peculiarities of oogenesis of many Black Sea fishes. Many years later, she recalled her work at Karadag and her unexpected discovery: females of a small coastal fish, the red mullet, were able to spawn daily during the whole spawn season of 3 to 3.5 months a year. Such a long spawning period had not been previously identified for any Black Sea fishes; the generally accepted consensus was that most species spawned just once per season.

Discovery and further research into multi-portion spawning of Black Sea fishes allowed a reevaluation of their fecundity leading to a significant increase in their understood reproductive potential.

Karadag became more than the place for Lidiya Oven's first scientific discoveries. After moving there for work, she met a young employee of the hydrometeorological station in the village of Kurortnoye, Evgeny Oven. Soon after, they got married and lived a happy life together since. They were united by a love for the natural wonders of Karadag, the Crimea, and the Black Sea.

After successfully defending her thesis and receiving a PhD in biology from the Odessa State University in 1963, L. Oven began a new position at the A. O. Kovalevsky Institute of Biology of the Southern Seas in Sevastopol.

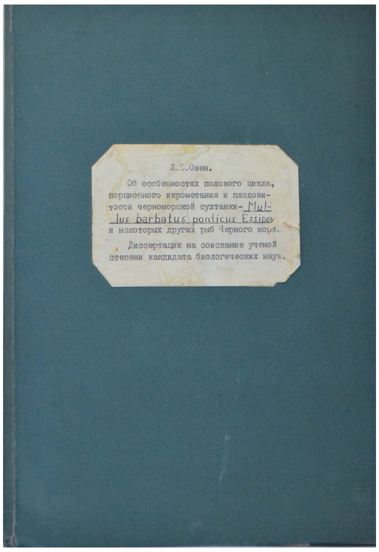
Since 1964, her entire career was connected with IBSS: here, she charted the path from a junior researcher to head of the department of ichthyology.

Lidiya Oven's main research interests included studies of reproductive biology of fish with a focus on gametogenesis, sexual maturation, formation of fecundity, and analysis of the effects of anthropogenic pollution of aquatic environments on these processes [70-letie, 2000].

Uncovering and studying of the process of multi-portion spawning in marine fish has changed the collective understanding about their reproductive potential. L. Oven showed that during a spawning season, oocytes of not only trophoplasmic but also protoplasmic growth can mature and be spawned; this significantly increases the overall seasonal fish fecundity.

She summarized the results of many years of research in the monograph *Features of Oogenesis and Characteristics of the Spawning of Marine Fish* [1976]. The book presents data on reproduction of members of 18 families of Black Sea fish and 7 families of tropical and subtropical fish from waters of the Atlantic, Indian, and Pacific oceans. Material for this work had been sampled from the Indian and Atlantic oceans, the Black, Mediterranean, and Red seas, and the Sea of Azov between 1955 and 1973. This collection of data was the result of comprehensive observation of maturation and spawning of 38 marine species with pelagic and demersal eggs under both experimental and natural conditions. While working on the monograph, Lidiya Oven prepared histological samples of ovaries and testicles of 1,500 specimens of 89 fish species. For studies of egg size distribution, 100 to 700 yolk oocytes were measured in each ovary.

L. Oven suggested the use of the following main attributes to characterize and study the reproduction of multi-portion spawning fish: size distribution of oocytes in the ovaries of mature females, the portion coefficient, the ratio of yolk oocytes of different size groups, and the change in the maturity coefficient of females during the spawning period. She also stressed the need for simultaneous biometrical analysis of ovarian eggs, histological analysis of the gonads, and separate counting of maturated eggs and yolk oocytes by size groups.

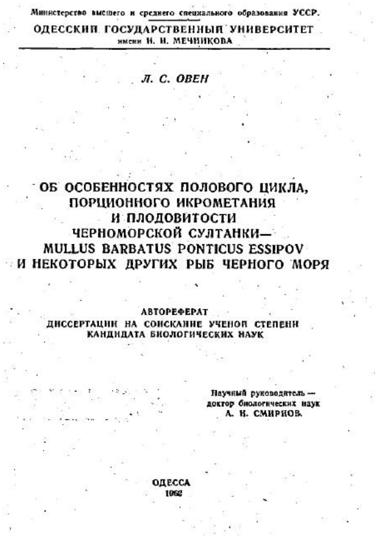


Л.С.Овен.

Об особенностях полового цикла, порционного икрометания и плодовитости черноморской султанки – *Mullus barbatus ponticus Essipov* и некоторых других рыб Черного моря.

Диссертация на соискание ученой степени кандидата биологических наук.

The cover of the PhD thesis of L. Oven (from the archive of the first author)



Министерство высшего и среднего специального образования УССР.
ОДЕССКИЙ ГОСУДАРСТВЕННЫЙ УНИВЕРСИТЕТ
имени И. И. МЕЧНИКОВА

Л. С. ОВЕН

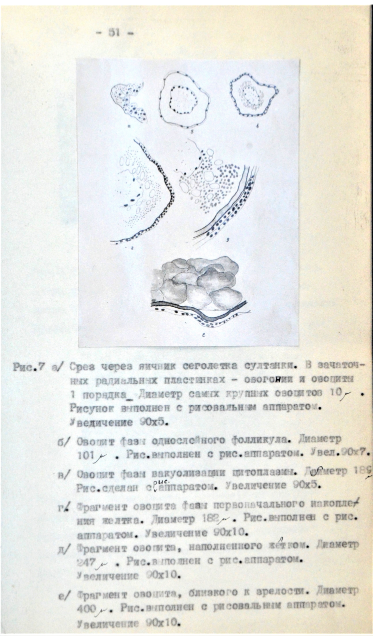
ОБ ОСОБЕННОСТЯХ ПОЛОВОГО ЦИКЛА,
ПОРЦИОННОГО ИКРОМЕТАНИЯ
И ПЛОДОВИТОСТИ
ЧЕРНОМОРСКОЙ СУЛТАНКИ—
MULLUS BARBATUS PONTICUS ESSIPOV
И НЕКОТОРЫХ ДРУГИХ РЫБ ЧЕРНОГО МОРЯ

АВТОРЕФЕРАТ
ДИССЕРТАЦИИ НА СОИСКАНИЕ УЧЕНОЙ СТЕПЕНИ
КАНДИДАТА БИОЛОГИЧЕСКИХ НАУК

Научный руководитель —
доктор биологических наук
А. Н. СМИРНОВ.

ОДЕССА
1962

The title page of the PhD thesis abstract of L. Oven



- 51 -

Рис.7 а/ Срез через яичник сеголетка султанки. В зачаточных радиальных пластинках – овогонии и овоциты 1 порядка. Диаметр самых крупных овоцитов 10 μ. Рисунок выполнен с рисовальным аппаратом. Увеличение 90х5.

б/ Овоцит фазы однослойного фолликула. Диаметр 101 μ. Рис.выполнен с рис.аппаратом. Увел.90х7.

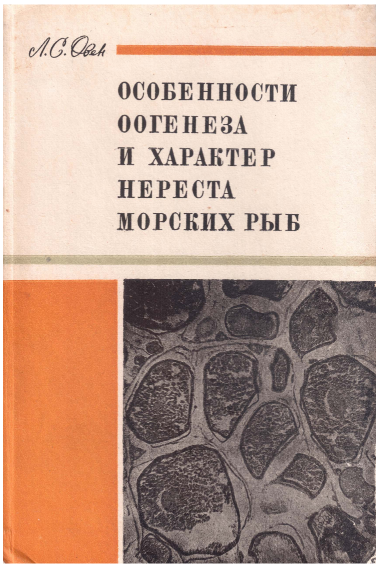
в/ Овоцит фазы вакуолизации цитоплазмы. Диаметр 189 μ. Рис.сделан с рис. аппаратом. Увеличение 90х5.

г/ Фрагмент овоцита фазы первоначального накопления желтка. Диаметр 182 μ. Рис.выполнен с рис. аппаратом. Увеличение 90х10.

д/ Фрагмент овоцита, наполненного желтком. Диаметр 247 μ. Рис.выполнен с рис.аппаратом. Увеличение 90х10.

е/ Фрагмент овоцита, близкого к зрелости. Диаметр 400 μ. Рис.выполнен с рисовальным аппаратом. Увеличение 90х10.

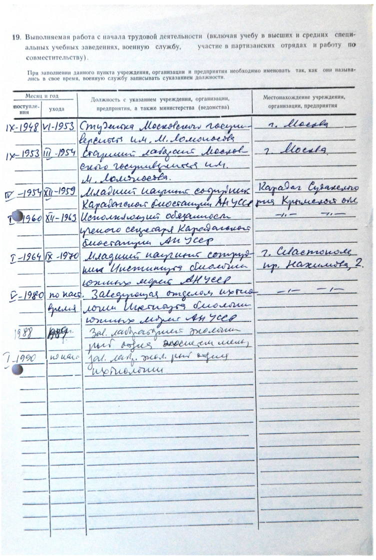
A figure from the PhD thesis of L. Oven. The drawings were made using a microscope and a drawing apparatus (from the archive of the first author)



Л.С.Овен

ОСОБЕННОСТИ
ООГЕНЕЗА
И ХАРАКТЕР
НЕРЕСТА
МОРСКИХ РЫБ

Cover of L. Oven's monograph, *Features of Oogenesis and Characteristics of the Spawning of Marine Fish*, published in 1976

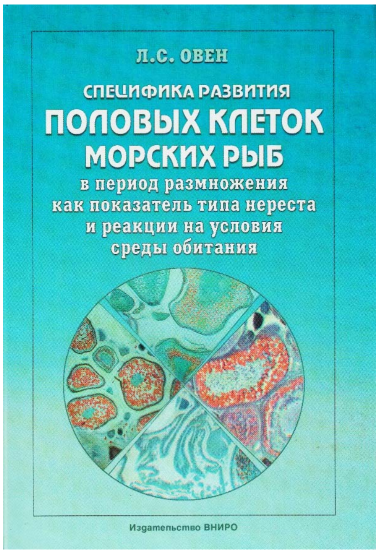


19. Выполняемая работа с начала трудовой деятельности (включая учебу в высших и средних специальных учебных заведениях, военную службу, участие в партизанских отрядах и работу по совместительству).

При заполнении данного пункта учреждения, организации и предприятия необходимо именовать так, как они назывались в свое время, военную службу записывать суказанием должности.

Месяц и год		Должность с указанием учреждения, организации, предприятия, а также министерства (ведомства)	Местонахождение учреждения, организации, предприятия
поступления	ухода		
IX-1948	VI-1953	Студентка Московского госуниверситета им. М. Ломоносова	г. Москва
IX-1953	III-1954	Старший лаборант Московского госуниверситета им. М. Ломоносова.	г. Москва
IV-1954	XII-1959	Младший научный сотрудник Карадагской биостанции АН УССР	Карадаг Судакского р-на Крымской обл.
I-1960	XII-1963	Исполняющий обязанности ученого секретаря Карадагской биостанции АН УССР	—"— —"—
I-1964	IX-1970	Младший научный сотрудник Института биологии южных морей АН УССР	г. Севастополь пр. Нахимова, 2.
V-1980	по наст. время	Заведующая отделом ихтиологии Института биологии южных морей АН УССР	—"— —"—
1988	1989	Зав. лабораторией экологии рыб отдела [illegible]	
I-1990	по наст.	Зав. лаб. экол. рыб отдела ихтиологии	

Records on the scientific career from the human resources department form filled by L. Oven (from the archive of the first author)



Л.С. ОВЕН

СПЕЦИФИКА РАЗВИТИЯ
ПОЛОВЫХ КЛЕТОК
МОРСКИХ РЫБ
в период размножения
как показатель типа нереста
и реакции на условия
среды обитания

Издательство ВНИРО

Cover of L. Oven's second monograph, *Specificity of the Development of Gametes in Sea Fish Reproduction as an Indicator of Spawning Type and Their Reaction to Environmental Conditions*, published by VNIRO in 2004

Staff of IBSS ichthyology department. Left to right: G. Zuev, A. Tkach, T. Dekhnik, E. Kalinina, A. Gordina, and L. Oven [Lidiya Oven: put' nauki i prosveshcheniya, 2024]

Staff of IBSS ichthyology department. Left to right: A. Gordina, L. Salekhova, L. Oven, and N. Shevchenko [Lidiya Oven: put' nauki i prosveshcheniya, 2024]

It is also worth noting the modification of R. Mailyan's method for counting eggs in the ovaries of marine fish made by L. Oven in her research.

In 1978, Lidiya Oven successfully defended her D. Sc. thesis *Peculiarities of Gametogenesis and Spawning Strategies of Marine Fish* before the dissertation committee at the Institute of Evolutionary Morphology and Ecology of Animals (now, the Severtsov Institute of Ecology and Evolution Problems of the RAS).

She was never the type to hole up in her office shying away from fieldwork and getting dirt under her fingernails. In the course of her career, she participated in seven major scientific expeditions – to the Black, Red, and Mediterranean seas, as well as to the Atlantic and Pacific oceans – aboard the RVs "Akademik A. Kovalevsky" and "Professor Vodyanitsky." Three times, she lead the research expeditions [70-letie, 2000].

For many years, L. Oven was a member of the IBSS scientific council. She served on the editorial boards of *Ecology of the Sea*, a scientific anthology issued by IBSS, and the *Journal of Ichthyology*, a renowned Russian journal.

During the 1990s, her studies focused on the effect of the anthropogenic transformation of the Black Sea ecosystem on the reproductive systems of fish. In fact, she laid the foundation for a new direction of research: bioindication of the state of the marine environment by analyzing the state of fish gonads.

Lidiya Oven published her second monograph through the VNIRO publishing house [2004]. In this book, she described reproduction characteristics of 17 families of fish with pelagic eggs and 8 families of fish with demersal eggs. Data presented in the monograph showed that portioned spawning is a characteristic shared by a substantial number of marine fish of temperate, tropical, and subtropical latitudes. In most marine polycyclic fish species, oocytes grow asynchronously during oogenesis developing according to one of two types – intermittent or continuous. Fish with intermittent type of oogenesis may have single spawning and two-, three-, or even multi-portion spawning. Fish with continuous oogenesis spawn in multiple portions.

She continued to conduct research and to mentor young scientists at IBSS even long after her well-deserved retirement.

Some personal reflections

Life had connected us with Lidiya Oven at the end of the 1980s and then scattered us to different cities and even countries, but we, her grad students, still keep very fond memories of our teacher.

Tatiana Bagnyukova, PhD

I entered the correspondence PhD program at IBSS in 1988 after graduating from the Odessa State University. The Karadag Biological Station, transformed by that time into the Karadag Natural Reserve, was my first workplace. Advised by L. Oven, I based my investigation of fish reproduction on her work conducted in the same region almost 40 years earlier. As a result, a comparative study came together demonstrating that the deterioration of reproductive characteristics of some Black Sea fish in the period from the late 1980s to the first half of the 1990s compared to the 1950s was well explained by anthropogenic pollution of coastal waters at the end of the 20th century.

I remember with great warmth my interactions with Lidiya Oven. I was struck by the lively sparkle in her eyes, the genuine interest in my work and in Karadag, where her own career had started. I remember with what delight she described her boat trips to sample ichthyoplankton and how insistently she advised me to work with live, unfixed samples for species identification in order to see the whole palette of colors and shades of eggs and larvae that are typically bleached by formalin. And indeed, the vibrant living world I saw under binocular microscope was amazing!

Histological slides of fish ovary I sampled at Karadag caused a kind of furor. I analyzed the fish species that were studied by L. Oven in the 1950s in detail: the red mullet, horse mackerel, European seabass, picarel, *etc.* Numerous photos of similar histological slides of the same species were included in her monograph published in 1976. Interestingly, the histology of fish ovaries collected in 1989–1991 was strikingly different from the "old" set of slides: the newer set showed signs of resorption of maturing oocytes up to their full destruction as well as other multiple pathologies of egg development. The situation near Karadag, as in all coastal water areas of the Black Sea, had changed with increasing pollution primarily affecting the most sensitive early stages of fish ontogenesis. This part of my study, performed with the direct supervision of Lidiya Oven, was the best part of my PhD thesis, according to many specialists.

I want to commend the incredible patience she had when working with my first attempts to write papers and then, my thesis. Few people can express their thoughts and describe results of their research at the beginning of their careers, and a mentor has the difficult task to teach their PhD student this as well. Lidiya Oven jokingly called the style of my first drafts, especially the early version of my thesis, "German." I tried to put as much information as possible into one phrase; my texts were so full of compound and complex sentences that often there were not more than two or three sentences *per* printed page. She did much to improve my writing style.

L. Oven, even at the mature age when I met her, was a person with a young soul. She remains in my memory as a very gentle, kind person, who did not allow any harsh comments about other people. She was one of several people thanks to whom I did not leave research in the difficult 1990s. Although I have since changed my research field, I still feel the benefits of her mentorship and the strong foundation laid down when she guided my work.

About the author: T. Bagnyukova was a PhD student of Lidiya Oven in 1988–1992. She graduated from the Odessa State University in 1988 and was distributed to work at the Karadag Natural Reserve. She entered the correspondence PhD program at IBSS (Sevastopol) the same year.

In 1996, she defended PhD thesis *Dynamics of Reproductive Characteristics and Spawning Intensity of Mass Species of the Black Sea Fish near Karadag* (adviser, L. Oven). Then, she conducted research on glycolytic enzymes under different physiological conditions, as well as oxidative processes and antioxidant enzymes of fish and amphibians under stress factors. Later, she studied epigenetic mechanisms of development of some cancer types at the National Center for Toxicological Research (Jefferson, AR, USA). Since 2009, T. Bagnyukova has studied molecular mechanisms of drug resistance and novel approaches for cancer treatment at the Fox Chase Cancer Center (Philadelphia, USA).

Andrei Pashkov, PhD

In the 1970–1980s, graduates of the Kuban State University faculty of biology were often sent to work at IBSS in Sevastopol. Upon learning that I grew up in a seaside town, my university mentor Yu. Abaev contacted Lidiya Oven and recommended me for a summer student position in her lab.

I remember well my first meeting with her in her office. She had heard that I liked diving and said: "There are nice people working at our biological station in Batiliman. When they have scuba-dived, they found a lot of new things – for example, that the sea scorpions "run" on the sand at night. I think you belong there."

For training, I was assigned to a junior research M. Kruglov. Both Lidiya Oven's lab staff (V. Giragosov, T. Klimova, N. Shevchenko, and T. Chesalina) and specialists from other IBSS departments (A. Petrov and N. Revkov) provided assistance with my work.

Material collected under her supervision during that period became the basis for my diploma thesis, and later, expanded and supplemented during my PhD program, the basis of my dissertation *Ichthyofauna of the Black Sea Shelf in Polyhaline Waters*. L. Oven helped me to define the key direction of my research: the study of species composition and biological features of coastal Black Sea fish based on a combined method of sampling including net fishing and conduction of visual underwater observation.

As my PhD program was conducted via correspondence and there was no opportunity to make long-distance phone calls or use the Internet that time, Lidiya Oven and I communicated mainly using regular mail. After discussing with her main concerns and plans for sampling, material processing, and its analysis during my visits to Sevastopol two or three times *per* year, I would then return to the biological station of the Kuban State University (Betta farm) from where I corresponded with her by mail. For me, those letters were an invaluable source of ideas and a guiding example of a competent approach to the organization of research.

For Lidiya Oven, I had always been just Andrei whether I was in my 20s, 30s, or 50s – no matter if I was a student, teacher, or researcher. Since our first meeting and to our last phone conversation, she has addressed me with the formal "you."[1] An *a priori* respectful attitude towards colleagues, including her subordinates and scientific opponents, was one of her striking characteristics. I never heard her raise her voice at anyone.

L. Oven was very sensitive to the presentation of research results. I still remember the stern talking she gave to me after finding some typos in my diploma thesis which I had proudly presented to her before entering the PhD program.

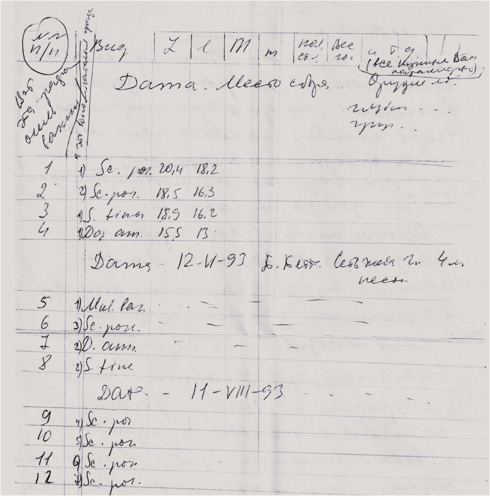
---

[1] There are two forms of "you" in Russian: a singular, informal "you" and a singular formal and plural "you." As a show of respect, people use the formal "you."

Even after retiring, she remained actively interested in my work, remembered the birthdays of my family members, and never forgot to send me holiday well wishes.

Lidiya Oven's support helped not to leave research in the 1990s and guided me in my life after that.

About the author: A. Pashkov was a PhD student of L. Oven in 1992–1996. He attended the Kuban State University in 1987–1992. In 1990–1992, he completed the summer program at IBSS (Sevastopol). After graduation in 1992, he started working at the Betta Biological Station of the Kuban State University; at the same time, he entered the correspondence PhD program at IBSS. In 1993–2001, he headed the Betta Biological Station, and after defending his PhD thesis in biology at "VNIRO," he worked as teacher, senior teacher, associate professor, and head of department at the Kuban State University. In 2016–2019, he was the deputy head of the Krasnodar Branch of the Azov Research Institute of Fisheries. Since 2019, he has been the leading researcher of the Krasnodar Department of the Azov–Black Sea branch of the "VNIRO" ("AzNIIRKh").



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1 1) Sc. por. 20,4 18,2
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8 2) S. tinca

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9 4) Sc. por
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11 6) Sc. por
12 7) Sc. por.

Fragment of a letter from L. Oven to the second author (1993)

The text of this paper has been approved by Lidiya Oven's daughter, Mariya Rubakhina.

The authors express their deep gratitude to Professor Irina Rudneva, D. Sc., for her help in preparing materials for the paper.

The main publications of Lidiya Oven are available in the IBSS open access repository (https://repository.marine-research.ru/).

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В ПАМЯТЬ О ЗАМЕЧАТЕЛЬНОМ ЧЕЛОВЕКЕ И ИХТИОЛОГЕ — ЛИДИИ СЕРГЕЕВНЕ ОВЕН

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В январе 2021 г. ушла из жизни Лидия Сергеевна Овен — замечательный человек и блестящий ихтиолог. Она внесла весомый вклад в ихтиологию, особенно в изучение репродуктивной биологии рыб, фактически заложив и развив методологические основы исследования особенностей оогенеза и характера размножения порционно нерестующих морских рыб. Не менее важными нам кажутся её человеческие, личностные качества. Мы, бывшие аспиранты Лидии Сергеевны, хотим почтить её память этим неформальным некрологом. Мы оба обучались в аспирантуре в сложное время — в первой половине 1990-х гг., когда само по себе решение стать учёным было нетривиальным. Вклад Л. С. Овен в формирование нас как учёных неоценим: она руководила нашими первыми шагами в науке и учила самостоятельно анализировать исследуемые биологические процессы. Данной публикацией мы хотим напомнить новым поколениям молодых биологов об этом прекрасном человеке.

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