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# FACTORS AFFECTING THE REPRODUCTION OF *LITTORINA OBTUSATA* POPULATION (GASTROPODA: LITTORINIDAE) IN THE WHITE SEA

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Studying the factors that affect the population size is necessary for understanding the functioning of natural ecosystems and for planning of measures for environmental protection and management. Periwinkles of the genus *Littorina* are an important component of the intertidal ecosystems in the Northern Hemisphere, but the factors involved in their population dynamics are still poorly understood. This paper presents the data obtained during monitoring surveys of *Littorina obtusata* in 2001–2020. During this period, quasi-cyclic changes in periwinkles population density were observed around the average level, which is about 2.6 thousand ind.$\cdot$m$^{-2}$. A total of 67 variables characterizing the state of the studied *L. obtusata* population and the effect of key environmental factors were analyzed. Fluctuations in recruitment were found to account for 83% of observed changes in population density. Multiple regression analysis showed that 78% of changes in the reproduction rate of *L. obtusata* population were determined by four variables: density of individuals aged two years and older, biomass of a brown alga *Fucus vesiculosus*, precipitation in July, and biomass of a bivalve *Mytilus edulis*. The first variable reflects the rate of intraspecific competition, the second, the ability of a given habitat to support a mollusc population of a certain size, and the third, the effect of environmental factors. The connection between the reproduction rate of periwinkle population and bivalve biomass can be explained either by the existence of some common factor with which both variables are correlated, or by the presence of interspecific interactions between *M. edulis* and *L. obtusata*.

**Keywords:** *Littorina obtusata*, population size, fluctuations in abundance, environmental factors, intraspecific competition, interspecific competition, habitat capacity

Fluctuations in abundance have been identified in populations of a wide range of animals: mammals, birds, insects, and molluscs [Bachelet, 1986; Baltensweiler, 1964; Elton, 1942; Lack, 1966; MacLulich, 1937; Maximovich, Gerasimova, 2004]. They were found to be driven by changes in food abundance, the impact of predators and parasites, intraspecific competition, and genetic heterogeneity of a population [Hudson et al., 1998; Högstedt et al., 2005; Kozminsky, 2013, 2017, 2020; Maximovich, Gerasimova, 2004; Sinclair et al., 2003]. However, the causes of population fluctuations have not been established in all known cases, and the underlying mechanisms are far from being fully understood.

Analyzing the factors that mediate changes in population size is necessary for a better understanding of the functioning of natural ecosystems and for planning measures of environmental protection and management. Therefore, it is important to cover with relevant studies as wide a range of animals as possible.

A key component of littoral ecosystems of the seas of the Northern Hemisphere are gastropods of the genus *Littorina* A. Férussac, 1822. On the one hand, they consume microfouling and littoral macrophytes; on the other hand, they are food for coastal fish and waterfowl. *Littorina* are the first intermediate host for several trematode species [Galaktionov, Dobrovolsky, 1984; Granovitch et al., 2000; Sergievsky, 1985] that cause epizootics in waterfowl, in particular the common eider *Somateria mollissima* (Linnaeus, 1758) [Kulachkova, 1960, 1979]. Being common littoral species, these molluscs are also a promising object for assessing the state of the environment.

The factors determining the population dynamics of periwinkles are poorly understood, the same as the corresponding mechanisms. Only in a few cases, not only such factors were identified, but also their contribution to the population dynamics was assessed. Thus, in the course of long-term observations [Kozminsky, 2013, 2017, 2020], it was established as follows: one of the factors mediating changes in population density of *Littorina obtusata* (Linnaeus, 1758) is intraspecific competition for a resource – a brown alga *Fucus vesiculosus* Linnaeus, 1753 – under conditions of limited habitat capacity. Intraspecific competition for food resources with an increase in mortality and a decrease in the growth rate of molluscs was revealed in some other *Littorina* species as well: *L. unifasciata*, *L. plena*, and *L. littorea* [Branch, Branch, 1981; Chow, 1989; Petraitis, 2002]. A number of studies have shown that the dynamics of the periwinkle population may be affected by such factors, as temperature [Chow, 1989; Kozminsky et al., 2008] and seawater salinity [Rusanova, Khlebovich, 1967; Sokolova, 1997, 2000], although their contribution to the long-term dynamics of population has not been assessed. There are data on interspecific competition between cohabiting periwinkle species as a possible cause of fluctuations in their abundance [Kozminsky, 2020]. As shown in some cases, parasitic pressure from digenetic flukes can result in a significant drop in the population reproduction rate [Brown et al., 1988; Kohler, Wiley, 1992]. However, long-term investigations have not revealed the effect of infection on the reproduction rate of *Littorina* populations [Granovitch, Maximovich, 2013; Kozminsky, 2020; Sergievsky et al., 1997].

This paper provides data obtained during long-term (2001–2020) observations on *Littorina obtusata* population dynamics. During this period, quasi-cyclic changes in the periwinkle population density were observed around the average level of about 2.6 thousand ind.·m$^{-2}$. The aim of our work was to identify factors governing the revealed fluctuations in abundance of this White Sea mollusc.

## MATERIAL AND METHODS

The material for the study was sampled on the western spit of the Southern Bay of Ryazhkov Island (67°00′N, 32°34′E; Kandalaksha State Nature Reserve) located in the apex of Kandalaksha Bay of the White Sea. The Southern Bay is oriented toward Kandalaksha Bay exit and protected from the open sea by a number of islands; therefore, it is characterized by a moderate level of wave action.

The surveyed area of the littoral zone is bounded below by zero depth and above by a littoral bath lined with fine sand and strewn with small stones. The sediment in the surveyed area is chiefly fine and medium gravel, with an admixture of moderately silted sand. The littoral zone is covered with different-sized stones, up to boulders of 1.5 m. Most of the biotope, approximately to 20 m from zero depth, is the zone of *F. vesiculosus* growth. In the area of zero depth, this alga forms mixed thickets with *Ascophyllum nodosum*. The fauna of invertebrates in the surveyed habitat is typical for the rocky littoral of the White Sea [Naumov, Olenev, 1981]. In some spots, species characteristics of the silted littoral zone are found in small quantities as well (molluscs *Peringia ulvae* and *Macoma balthica* and a sea cucumber *Chiridota laevis*).

The material was sampled annually in 2001–2020 between 10 August and 6 September. Quantitative samples were taken from plots of 1/40 $m^2$ arranged in series of three along the transect at levels of 0, 5, 10, 15, 20, and 25 m. During sampling, macrophytes (if present) and the upper sediment layer were removed from the plots. The samples were transported to a laboratory; there, they were washed with freshwater using a sieve with a mesh diameter of 0.6 mm and quantitatively sorted. For each sample, we determined the wet weight of the brown algae *F. vesiculosus* and *A. nodosum* (by species, with an accuracy of ±0.5 g), filamentous algae[*] (with an accuracy of ±0.1 g), and mollusc species found: *Littorina saxatilis* (±1 mg), *L. obtusata* (±1 mg), *Mytilus edulis* (±0.5 g), and *P. ulvae* (±1 mg). Also, we counted the total number of registered periwinkles.

The total biomass of *L. obtusata* aged one year and older was determined by weighing molluscs. In the case of recruits (0+), due to their small size, the shell diameter–weight relationship was first constructed and then used to calculate the individual weight of specimens and to refine the total biomass. Notably, biomass of recruits is low (0.7% on average) compared to the total biomass of periwinkles aged one year and older.

For each *L. obtusata*, the maximum shell diameter (±0.1 mm) was recorded, and age was determined based on the annual rings on a shell [Kozminsky, 2006]. When indicating age, we used the following designations: recruits (individuals born during the current year), 0+; molluscs aged one year (born in the previous year), 1+; molluscs aged two years (born in the penultimate year), 2+; *etc.*

By dissecting the molluscs, we determined their sex, the state of the reproductive system (rudimentary, underdeveloped, normal, or reduced), and infection with trematode parthenitae.

The White Sea *L. obtusata* serve as the first intermediate host for a number of trematode species [Galaktionov, Dobrovolsky, 1984; Granovitch et al., 2000; Sergievsky, 1985]. All detected species of flukes cause complete parasitic castration [Galaktionov, 1993; Ganzha, Granovich, 2008; Granovitch, Sergiyevsky, 1990] and affect the reproduction of the host population to one degree or another. Since the purposes of this study required an assessment of only the total parasitic pressure on the reproduction of the periwinkle population, the prevalence of mollusc infection with all trematode species was used as the corresponding indicator.

Meteorological data on the state of the environment during the study period (air temperature, precipitation, and sunshine duration) from the nearby weather station Kandalaksha (No. 22217) were taken from the website of the All-Russian Research Institute of Hydrometeorological Information (http://meteo.ru/data). The values of the North Atlantic Oscillation index, NAO (annual, seasonal, and monthly) were obtained from the website of the US National Center for Atmospheric Research (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based).

During the work, four groups of variables were analyzed; those characterize the state of the studied *L. obtusata* population and its habitat conditions.

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[*] Approximately ¾ are *Cladophora* sp. and ¼ are *Stictyosiphon* sp.

The first group covers the indicators featuring the state of the *L. obtusata* population (10 pcs): biomass (g·m$^{-2}$) ($W_{LO}$); density (ind.·m$^{-2}$) of recruits (0+), molluscs aged one year (1+), molluscs aged two years (2+), molluscs aged two years (2+) and older, and molluscs aged three years (3+) and older ($D_{LO0+}$, $D_{LO1+}$, $D_{LO2+}$, $D_{LO\geq2+}$, and $D_{LO\geq3+}$, respectively); density of males with normally developed penis ($D_{PN}$) and mature uninfected females ($D_{FRT}$); the ratio of abundance of males to abundance of females among mature uninfected individuals ($R_{ML/FML}$); and the average shell diameter of mature uninfected females (mm) ($X_D$).

The second group includes indicators of the population state of the cohabiting species *L. saxatilis* (5 pcs): biomass (g·m$^{-2}$) ($W_{LS}$); density (ind.·m$^{-2}$) of recruits (0+), molluscs aged one year (1+), molluscs aged two years (2+), and molluscs aged three years (3+) and older ($D_{LS0+}$, $D_{LS1+}$, $D_{LS2+}$, and $D_{LS\geq3+}$, respectively).

The third group covers indicators characterizing the biotic habitat conditions of molluscs (6 pcs): biomass (g·m$^{-2}$) of the brown algae *F. vesiculosus* ($W_{FV}$) and *A. nodosum* ($W_{AN}$), filamentous algae ($W_{FA}$), and molluscs *M. edulis* ($W_{ME}$) and *P. ulvae* ($W_{PU}$); prevalence of infection with trematode parthenitae (%) (PI).

The fourth group includes indicators featuring the environmental conditions during the study period (45 pcs): values of the North Atlantic Oscillation index for a year, by season, and for a month ($NAO_{AN}$, $NAO_{JJA}$, $NAO_{JAS}$, $NAO_{ASO}$, $NAO_{JUN}$, $NAO_{JUL}$, $NAO_{AUG}$, and $NAO_{SEP}$); air temperature (°C) average for a year, for a period of several months, and for a month ($T_{AN}$, $T_{V–IX}$, $T_{V–X}$, $T_{VI–IX}$, $T_{VI–X}$, $T_{XI–IV}$, $T_{XI–V}$, $T_V$, $T_{VI}$, $T_{VII}$, $T_{VIII}$, $T_{IX}$, and $T_X$); amount of precipitation (mm) for a year, in the cold and warm period, and for a month ($H_{AN}$, $H_{V–IX}$, $H_{V–X}$, $H_{VI–IX}$, $H_{VI–X}$, $H_{XI–IV}$, $H_{XI–V}$, $H_V$, $H_{VI}$, $H_{VII}$, $H_{VIII}$, $H_{IX}$, and $H_X$); and sunshine duration (h) for a year, for a period of several months, and for a month ($DS_{AN}$, $DS_{V–IX}$, $DS_{V–X}$, $DS_{VI–IX}$, $DS_{VI–X}$, $DS_V$, $DS_{VI}$, $DS_{VII}$, $DS_{VIII}$, $DS_{IX}$, and $DS_X$).

Generally accepted statistical methods were applied. When checking for normality, we used the Kolmogorov–Smirnov test (the Lilliefors probabilities were calculated [Lilliefors, 1967], as the parameters of the normal distribution were estimated based on sample data) and the Shapiro–Wilk test. Correlation analysis was applied for preliminary selection of data (filtering) for multiple regression analysis. Since almost all the considered indicators (with rare exceptions) were normally distributed ones, the Pearson correlation coefficient ($R$) was used to estimate the degree of relationship between them. The correlation of non-normally distributed variables with abundance of recruits was estimated by the Spearman's rank correlation coefficient ($R_S$). Multiple regression analysis was applied to identify factors affecting the reproduction of the *L. obtusata* population. All calculations were performed in Statistica 7.0.

## RESULTS

During the study period, quasi-cyclic changes in *L. obtusata* population density were observed around the average level of 2,620 ind.·m$^{-2}$ (Fig. 1A). Fluctuations in abundance of recruits accounted for 82.5% of the population changes ($R = 0.908$; $\alpha << 0.001$). Densities of periwinkles aged one year, periwinkles aged two years, and sexually mature molluscs (≥ 3+) generally followed them with a corresponding shift (Fig. 1B–E). Thus, revealing the factors that mediate changes in the *L. obtusata* population size comes down to analyzing the causes of fluctuations in abundance of recruits ($D_{LO0+}$).

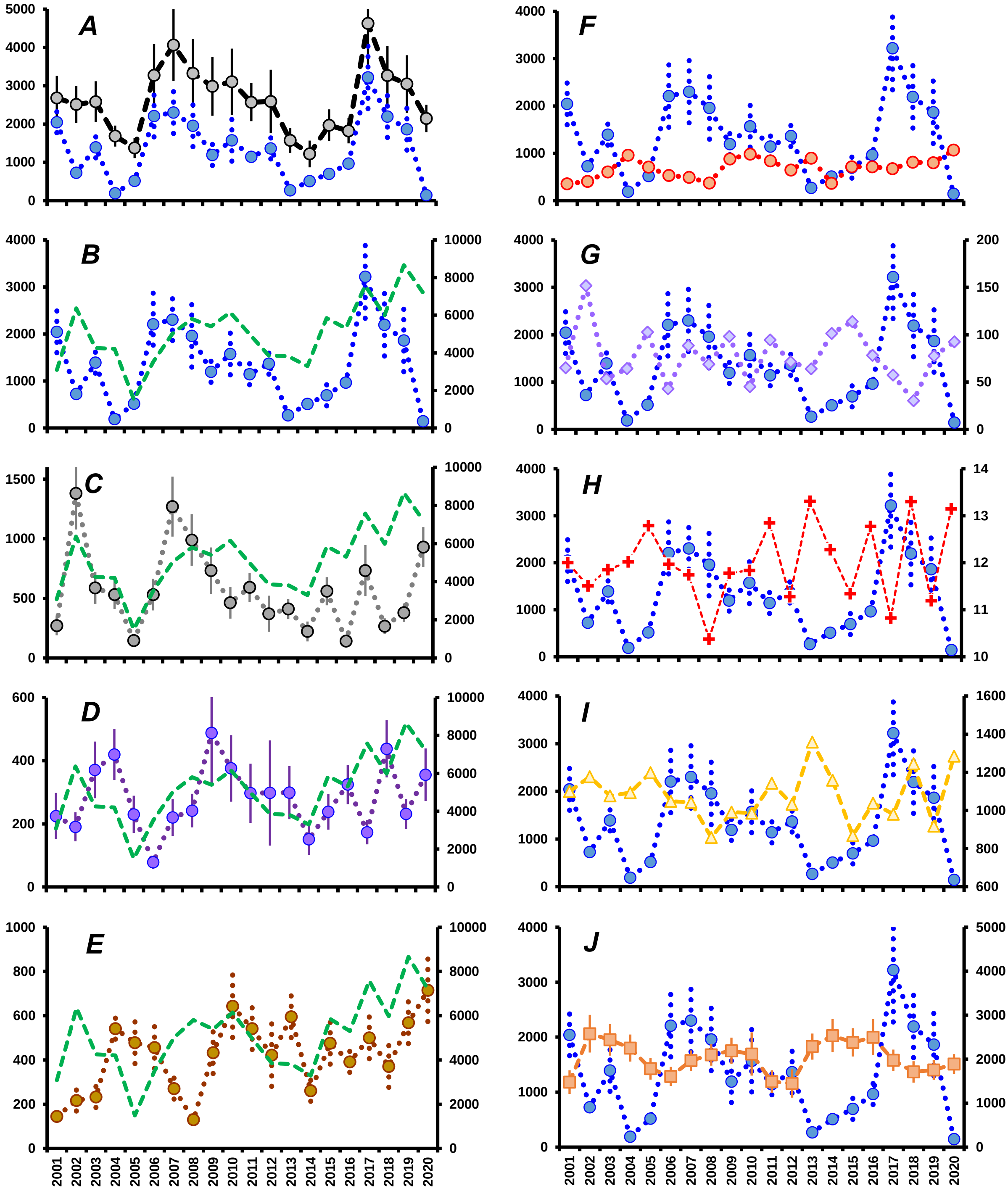

**Fig. 1.** Dynamics of changes in density of different age groups of *Littorina obtusata* (A–F) and environmental factors (G–J) during the study period. The dotted lines (◯ marker) denote different age groups of molluscs: black, the entire population; blue, 0+; gray, 1+; purple, 2+; red, ≥ 2+; and brown, ≥ 3+. The dashed lines denote the variables: lilac, $H_{VII}$ (♦); red, $T_{VI–IX}$ (+); yellow, $DS_{V–IX}$ (▲); orange, $W_{ME}$ (■); and green, $W_{FV}$ (no marker). Variables and age groups are explained in the text. On the abscissa axis, years are shown. On the left ordinate axis, the density of individuals is shown (ind.$\cdot$m$^{-2}$). On the right ordinate axis, the values of environmental factors are shown: biomass (g$\cdot$m$^{-2}$), precipitation (mm), temperature (°C), and sunshine duration (h). The standard errors of the mean are indicated

**Normality test.** The vast majority of variables were normally distributed. The exceptions were three indicators: density of *L. saxatilis* recruits ($D_{LS0+}$), *A. nodosum* biomass ($W_{AN}$), and sunshine duration in September ($DS_{IX}$).

**Data filtration.** At the first stage, by correlation analysis, we selected relevant indicators, *i. e.*, those noticeably correlated with the analyzed variable ($D_{LO0+}$). For certainty, we considered the values of correlation coefficients higher than or equal to $|0.30|$ to be significant; this corresponds to the contribution of the analyzed indicators to the variability of the dependent variable of about 10% (notably, the values of the correlation coefficients higher than or equal to $|0.45|$ were statistically reliable at the 5% confidence level). The correlation of $NAO_{ASO}$ with the density of *L. obtusata* recruits was formally a little lower than the accepted critical level ($R = +0.27$); however, we retained this variable in the analysis as an integral indicator featuring weather conditions in the second half of the warm period. When testing the correlation level between abundance of *L. obtusata* recruits and three non-normally distributed variables ($D_{LS0+}$, $W_{AN}$, and $DS_{IX}$) with the Spearman's rank correlation coefficient, we found that it was lower than the accepted critical value, $|0.30|$. As a result, 18 variables were considered relevant: $W_{LO}$, $D_{LO\geq2+}$, $D_{LO\geq3+}$, $D_{PN}$, $W_{FV}$, $W_{ME}$, $H_{VII}$, $H_{IX}$, $NAO_{JUL}$, $NAO_{ASO}$, $DS_{V-IX}$, $DS_{V-X}$, $T_{VI}$, $T_{IX}$, $T_{VI-IX}$, $T_{VI-X}$, $T_{V-IX}$, and $T_{V-X}$.

Then, the relevant variables were checked for redundancy. The indicators significantly associated ($\alpha < 0.05$) with other variables selected for the analysis were excluded if they were less strongly correlated with the dependent variable ($D_{LO0+}$) or – with a similar strength of correlation – were less preferable for use in the analysis. $T_{VI}$, $T_{IX}$, $T_{VI-X}$, $T_{V-IX}$, and $T_{V-X}$ were excluded from further analysis, because they were significantly correlated with $T_{VI-IX}$. The latter, in turn, was excluded, as it was significantly correlated with the density of molluscs aged two years and older ($R = 0.45$; $\alpha = 0.049$). Out of four variables featuring the state of the *L. obtusata* population ($D_{LO\geq2+}$, $D_{LO\geq3+}$, $W_{LO}$, and $D_{PN}$), abundance of molluscs aged two years and older was most strongly associated with the density of recruits ($R = 0.35$; $\alpha = 0.133$). Three other variables were significantly correlated with this indicator ($R \geq 0.80$; $\alpha << 0.001$) and were excluded from the analysis. Sunshine duration within May–October ($DS_{V-X}$) was excluded, for it was noticeably correlated with $DS_{V-IX}$ ($R = 0.99$; $\alpha << 0.001$) – the variable more precisely reflecting the idea of a warm period. Finally, the amount of precipitation in September ($H_{IX}$) was significantly correlated with *F. vesiculosus* biomass ($R = 0.46$; $\alpha < 0.044$). As a result, seven indicators ($D_{LO\geq2+}$, $W_{FV}$, $W_{ME}$, $H_{VII}$, $DS_{V-IX}$, $NAO_{JUL}$, and $NAO_{ASO}$) were selected for further analysis; there was no significant relationship between them (Table 1).

**Table 1.** Pearson correlation coefficients between the variables selected for multiple regression analysis

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| $D_{LO0+}$ | – | | | | | | | |
| $H_{VII}$ | **−0.50** | – | | | | | | |
| $DS_{V-IX}$ | **−0.46** | 0.04 | – | | | | | |
| $NAO_{JUL}$ | 0.35 | −0.23 | 0.19 | – | | | | |
| $NAO_{ASO}$ | 0.27 | −0.24 | −0.01 | 0.06 | – | | | |
| $D_{LO\geq2+}$ | −0.35 | −0.20 | 0.24 | −0.12 | 0.15 | – | | |
| $W_{ME}$ | −0.41 | 0.37 | −0.03 | −0.03 | −0.15 | −0.07 | – | |
| $W_{FV}$ | 0.30 | 0.03 | −0.33 | 0.25 | 0.23 | 0.30 | 0.10 | – |
| | $D_{LO0+}$ | $H_{VII}$ | $DS_{V-IX}$ | $NAO_{JUL}$ | $NAO_{ASO}$ | $D_{LO\geq2+}$ | $W_{ME}$ | $W_{FV}$ |

**Note:** the coefficients at 5% confidence level are highlighted in bold. Variables are explained in the text.

**Selection of the regression model.** Since the correlation between the independent variables was low, we did not use variants of multiple regression analysis involving the regularization procedure to improve the stability of the model (ridge regression, lasso regression, and elastic net). We analyzed models with and without a non-zero intercept. In both cases, various methods of variable selection were used: forward stepwise selection of all variables, their backward stepwise selection, and forced stepwise selection. Models with a zero intercept were excluded due to their poor quality: a high standard error of the estimate (*SEE*), low tolerance of variables, and strong correlation between some regression coefficients and between residuals and independent variables.

**Results of regression analysis: Factors affecting population reproduction.** Analysis of regression models with a non-zero intercept and different numbers of variables showed that the overwhelming majority of models include two variables, $H_{VII}$ and $D_{LO\geq2+}$. When adding to such a “basic” model the variables $DS_{V–IX}$, $NAO_{JUL}$, and $NAO_{ASO}$ in various combinations, the corresponding regression coefficients did not significantly differ from zero. The highest values of the multiple correlation coefficient ($R = 0.881$) and the lowest standard error of the estimate ($SEE = 446.7$) were obtained for the equation involving four variables, $D_{LO\geq2+}$, $H_{VII}$, $W_{FV}$, and $W_{ME}$:

$$D_{LO0+} = -2.46 \times D_{LO\geq2+} + 0.26 \times W_{FV} - 15.63 \times H_{VII} - 0.73 \times W_{ME} + 4,363.37\,. \quad (1)$$

The plot corresponding to the model is given in Fig. 2. The obtained dependence allows us to explain 77.6% of the variability of the dependent variable. The value of $F$-criterion (the Fisher criterion) evidences for a high reliability of the approximation ($F(4,15) = 13.03$; $\alpha << 0.001$).

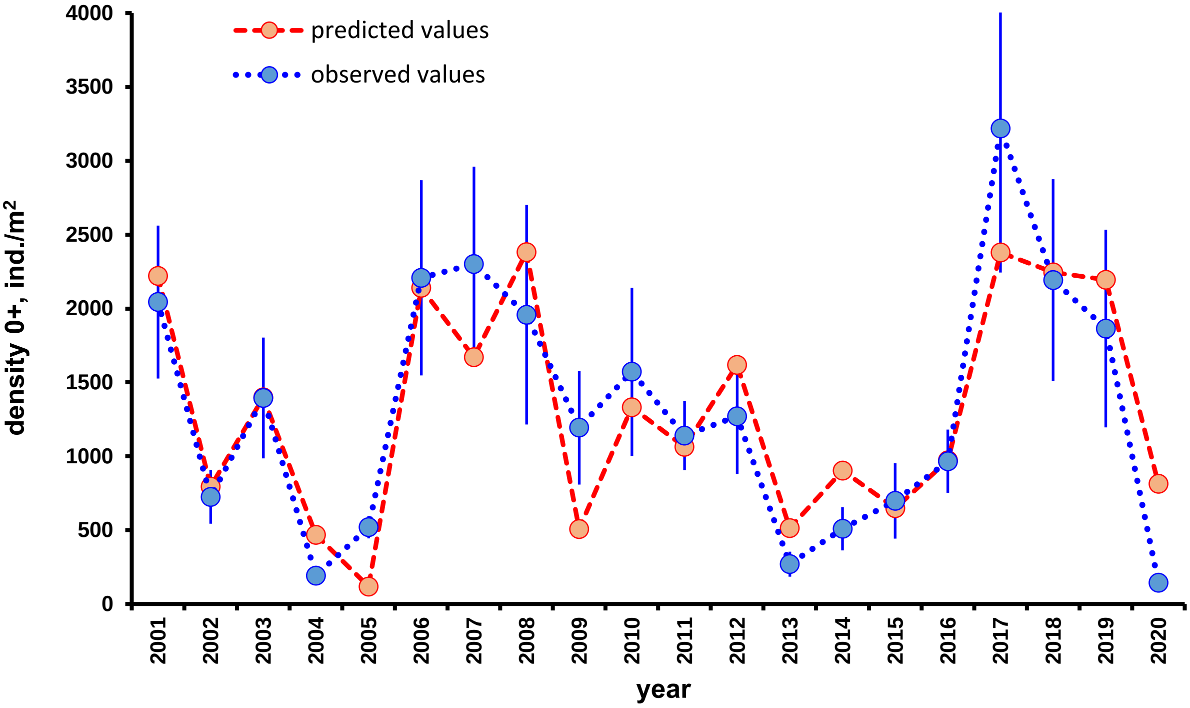

**Fig. 2.** The observed and predicted densities of *Littorina obtusata* yearlings. The standard errors of the mean are indicated

The analysis of the parameters (Table 2) evidences for a high quality of the model. All the main statistics were reliable at least at the 5% confidence level. The tolerance of all independent variables is quite high indicating a weak correlation between them. Apparently, the value of tolerance is affected by the presence of weak connections in two pairs of variables: $D_{LO\geq 2+}$ and $W_{FV}$ ($R = +0.30$) and $H_{VII}$ and $W_{ME}$ ($R = +0.37$). The correlation between the variables of different pairs is much weaker. Partial and semipartial correlations are high in all cases confirming the presence of a strong connection between the independent variables and a dependent one. The correlation between the regression coefficients is unreliable and does not exceed $|0.35|$. The analysis of the residuals showed a low level of correlation between them and the independent variables ($R$ was about $10^{-7}$). The residuals fit the straight line of the normal probability plot; the analysis of the distribution of the standardized residuals shows that they all are within $\pm 2\sigma$. Both indicators evidence for the fact that the residuals are normally distributed. The Cook's distance is moderately significant for three points alone (2005, 2017, and 2020), but the Mahalanobis distances and the distribution of standardized residuals show that there is no reason to consider these points as outliers.

Thus, our results indicate that during the study period, the reproduction rate of the *L. obtusata* population was affected by four variables: $D_{LO\geq 2+}$, $W_{FV}$, $H_{VII}$, and $W_{ME}$.

**Table 2.** The main parameters of the regression equation for the density of *Littorina obtusata* yearlings

| | BETA | $SE_{BETA}$ | B | $SE_B$ | $R_{PART}$ | $R_{SPART}$ | T | $t(15)$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|
| Int | | | 4,363.37 | 706.18 | | | | 6.18 | 0.0000 |
| $D_{LO\geq 2+}$ | −0.6376 | 0.1313 | −2.46 | 0.51 | −0.782 | −0.593 | 0.864 | −4.86 | 0.0002 |
| $W_{FV}$ | 0.5369 | 0.1292 | 0.26 | 0.06 | 0.731 | 0.507 | 0.892 | 4.15 | 0.0008 |
| $H_{VII}$ | −0.5265 | 0.1338 | −15.63 | 3.97 | −0.713 | −0.480 | 0.832 | −3.93 | 0.0013 |
| $W_{ME}$ | −0.3200 | 0.1318 | −0.73 | 0.30 | −0.531 | −0.296 | 0.858 | −2.43 | 0.0283 |

**Note:** BETA, regression equation coefficients calculated from standardized values of the variables; $SE_{BETA}$, standard errors of BETA; B, regression equation coefficients calculated from initial values of the variables; $SE_B$, standard errors of B; $R_{PART}$, partial correlations; $R_{SPART}$, semipartial correlations; T, tolerance; *t*, *t*-test value associated with the calculated statistics; $\alpha$, corresponding probabilities; and Int, intercept. Variables are explained in the text.

**Analysis of individual factors.** As shown by the value of the standardized regression coefficient (BETA = −0.6376) (Table 2), the density of individuals aged two years and older has the greatest effect on fluctuations in abundance of *L. obtusata* recruits. These variables are in relationships close to antiphase ones ($R = -0.35$; $\alpha = 0.133$) (Fig. 1F).

The second most important factor (BETA = +0.5369) affecting abundance of recruits is biomass of a brown alga *F. vesiculosus*. Although the correlation between *F. vesiculosus* biomass and density of *L. obtusata* recruits is not reliable ($R = +0.30$; $\alpha = 0.203$), it is obvious that abundance of recruits in general follows abundance of this alga (Fig. 2B), that is, the higher the *F. vesiculosus* biomass, the more juveniles survive. Against this backdrop, numerous chaotic deviations are observed which seem to be governed by the fact that the survival of *L. obtusata* recruits is affected by many factors. The above-mentioned trend is disrupted only at the very end of the study period (in 2018–2020). Abundance of molluscs aged one year also changed almost synchronously with *F. vesiculosus* biomass ($R = +0.40$; $\alpha = 0.082$) (Fig. 1C). Abundance of *L. obtusata* in the age group 2+, as well as 3+ and older, followed *F. vesiculosus* biomass with some lag (Fig. 1D, E). This indicates that with a high abundance of *F. vesiculosus*, more juvenile *L. obtusata* survive. Between 2014 and 2020, against the backdrop of a rapid gain in *F. vesiculosus* biomass, the density of molluscs at the age of 1+, 2+, and 3+ and older also increased.

The third important factor (BETA = –0.5265) comparable in strength of effect with *F. vesiculosus* biomass, is the amount of precipitation in July ($H_{VII}$). This variable reflects the effect of abiotic environmental factors on the reproduction of the mollusc population. The density of recruits is in antiphase with the amount of precipitation ($R = -0.50$; $\alpha = 0.026$) (Fig. 1G). Notably, abundance of *L. obtusata* recruits is negatively correlated with air temperature ($T_{VI–IX}$) ($R = -0.47$; $\alpha = 0.036$) (Fig. 1H) and with sunshine duration ($DS_{V–IX}$) ($R = -0.46$; $\alpha = 0.043$) (Fig. 1I) during the warm period. Both characteristics are significantly related to each other ($R = 0.84$; $\alpha << 0.001$), but are not correlated with the amount of precipitation in July.

The last factor in terms of strength of the relationship with the density of *L. obtusata* recruits (BETA = –0.3200) is *M. edulis* biomass. The same as the amount of precipitation, this variable is in relationships close to antiphase ones (Fig. 1J) with the density of recruits ($R = -0.42$; $\alpha = 0.069$). With the exception of three cases, no reliable correlations were found between *M. edulis* biomass and most of the other variables considered. The first exception is the positive relationship ($R = +0.53$; $\alpha = 0.017$) between *M. edulis* abundance and the amount of precipitation in the warm period ($H_{VI–IX}$). The second one is the negative correlation between the mussel biomass and the prevalence of periwinkle infection with trematode parthenitae ($R = -0.59$; $\alpha = 0.006$). The third exception is a positive relationship between *M. edulis* abundance and *L. saxatilis* biomass ($R = +0.72$; $\alpha < 0.001$).

## DISCUSSION

Long-term studies have revealed noticeable interannual fluctuations in the periwinkle population density with pronounced cyclicity [Kozminsky, 2013, 2017, 2020; Sergievsky et al., 1997]. Analyzing such fluctuations, S. Sergievsky *et al.* [1997] concluded that they are mediated by changes in the reproduction rate of the population. Our data are fully consistent with it: 82.5% of the registered fluctuations were governed by changes in abundance of recruits.

We have shown earlier [Kozminsky, 2013, 2017, 2020] that quasi-cyclic fluctuations in abundance are due to intraspecific competition between recruits and *L. obtusata* aged three years and older for a resource, *F. vesiculosus*, under conditions of limited habitat capacity. This brown alga is the main source of food for *L. obtusata* (both by itself and due to microfouling) and a substrate for habitation and oviposition [Beskupskaya, 1963; Matveeva, 1974]. Abundance of younger *L. obtusata* (0+ and 1+) follows *F. vesiculosus* abundance; therefore, this alga is a key resource limiting the periwinkle population size. The occurrence of intraspecific competition is evidenced by the existence of relationships close to antiphase ones between abundance of recruits and abundance and biomass of mature *L. obtusata* [Kozminsky, 2013, 2017, 2020].

The data obtained in the course of this study are in good agreement with the previous observations. The key role of *F. vesiculosus* as a resource limiting the mollusc population density is confirmed by coordinated changes in the periwinkle abundance and abundance of individual age groups (Fig. 1B–D). This is also indicated by the fact that *L. obtusata* biomass and *F. vesiculosus* biomass were reliably correlated ($R = +0.55$; $\alpha = 0.013$). The occurrence of intraspecific competition is confirmed by the presence of relationships close to antiphase ones between abundance of *L. obtusata* recruits and density of large molluscs – those aged two years and older (Fig. 1F). Interestingly, in this study, in contrast to earlier investigations [Kozminsky, 2013, 2017, 2020], the strongest negative correlation was revealed between densities of recruits and *L. obtusata* aged two years and older, not between recruits and mature individuals (≥ 3+). Apparently, this means that abundance of just large periwinkles is more important, than abundance of mature ones. Another detail worth noting is a rise (since 2014) in densities of molluscs aged 1+, 2+, 3+ and older against the backdrop of a sharp increase in *F. vesiculosus* biomass. These processes seem to reflect a gain in habitat capacity. Abundance of recruits also rose during this time (until 2018), but then dropped (clearly, due to an increase in density of large *L. obtusata*).

Thus, the first variable in the equation (1), abundance of molluscs aged two years and older, reflects the rate of intraspecific competition. The second one, *F. vesiculosus* biomass, reflects habitat capacity, *i. e.*, its ability to maintain *L. obtusata* population of a certain size.

The most important factor for marine animals is salinity. The zone of optimal salinity for the White Sea *L. obtusata* is limited by 34–36‰ from above and by 14–16‰ from below. The lower boundary of the transitional low salinity zone (at which some molluscs still remain active) is 6–8‰ [Berger, 1976b]. The same as in most marine animals [Berger, 1986; Kinne, 1971; Remane, Schlieper, 1972], in periwinkles, individuals in the early stages of ontogenesis are the most vulnerable to effects of unfavorable environmental factors. In a closely related species, *L. saxatilis*, the level of perinatal and juvenile mortality was found to rise under conditions of low salinity [Sokolova, 1997, 2000]. *L. obtusata* tolerance to a decrease in salinity varies throughout the year and peaks in spring and summer [Berger, 1976b].

The relationship between the amount of precipitation and the reproduction rate of the *L. obtusata* population seems to be mediated by salinity fluctuations during precipitation. The presence of a relationship between the amount of precipitation and salinity (level of desalination) is confirmed by data of V. Khaitov [2008; 2009; 2010]. The mean salinity in the summer of 2007, 2008, and 2009 in the Southern Bay of Ryazhkov Island was 18.8, 19.9, and 20.2‰, respectively, while the amount of precipitation in the period from November of the previous year to August of the current year (according to the weather station in Kandalaksha) was 561, 514, and 501 mm. Apparently, the effect of precipitation on *L. obtusata* juveniles is chiefly due to desalination of the surface layer of seawater immediately at the time of precipitation. Mass oviposition of *L. obtusata* occurs in late May–early July. The embryonic development of *L. obtusata* lasts about a month; accordingly, most juveniles hatch in late June–early July [Kozminsky, 2006; Kuznetzov, 1960; Matveeva, 1974]. It is logical to assume that *L. obtusata* juveniles are most sensitive to desalination immediately after hatching, and this seems to explain the negative correlation between the density of *L. obtusata* recruits and the amount of precipitation in July.

Thus, the third variable in the equation (1) characterizes the effect of environmental factors (in this case, precipitation) on the reproduction of the periwinkle population.

As shown by the obtained results, abundance of *L. obtusata* recruits also negatively correlates with temperature and sunshine duration during the warm period. Accordingly, the survival rate of juveniles should be lower in a warm and sunny summer. This conclusion is supported by both literature data and our own observations. Thus, as shown for *Littorina plena* [Chow, 1989], high temperature can be the cause of mass mortality of molluscs. With a rise in water temperature to values exceeding +22 °C, an increase in mortality of juveniles and frequency of embryonic malformations are observed in *L. obtusata* [Kozminsky et al., 2008]. Temperature is reliably correlated with sunshine duration. Obviously, in clear weather, air heats up more, and this results in more heating of the surface layer of seawater and surface of substrates during low tide. Both can govern a rise in mortality of juveniles. At the same time, sunshine duration seems to be significant on its own: in clear, sunny weather, the risk of death of fish juveniles due to desiccation increases.

However, none of the above-mentioned variables was involved in the obtained equation (1). Most likely, this is explained by the fact as follows: for *L. obtusata*, seawater salinity is more important than the possibility of overheating or desiccation. At the same time, both factors can come to the fore with a shift in conditions of the population's existence. Values of the North Atlantic Oscillation index ($NAO_{JUL}$ and $NAO_{ASO}$) were also not included in the equation (1). This seemed to happen, because these are integral indicators that latently "take into account" both precipitation and temperature; accordingly, the connection with them should be weaker.

The occurrence of a relationship between *M. edulis* biomass and the reproduction rate of the *L. obtusata* population is unexpected. It can be explained in two ways: the relationship can be governed by the presence of some common factor which both variables are correlated with and by the occurrence of interspecific interactions between *M. edulis* and *L. obtusata*.

In our opinion, out of the variables considered in this study, the only real candidate for the role of a common factor affecting both the reproduction of the *L. obtusata* population and *M. edulis* abundance is the amount of precipitation correlated with both the reproduction of the periwinkle population and *M. edulis* biomass. The negative relationship between the amount of precipitation and the reproduction rate of the mollusc population was discussed earlier. The positive correlation between the amount of precipitation and *M. edulis* biomass can be explained by a gain in the amount of biogenic elements entering Kandalaksha Bay with freshwater runoff from the mainland with an increase in the amount of precipitation, and, accordingly, a more rapid development of phyto- and zooplankton (the food for *M. edulis*). Moreover, we cannot rule out the occurrence of some common factor not taken into account in this study.

Competitive interactions between different mollusc species are quite common, although their occurrence seems to be species-specific, and interspecific competition has not been detected in many cases [Watz, Nyqvist, 2022]. Interspecific competition can result in separation of ecological niches of cohabiting mollusc species [Golikov et al., 2020; Kimura, Chiba, 2010], an increase in mortality [Baker, 2021; Espinosa et al., 2006], and changes in feeding intensity [Smallridge, Kirby, 1988], growth rate [Aguilera, Navarrete, 2012; Campbell et al., 2015; Yamada, Mansour, 1987], individual fecundity, and the reproduction rate of a population [Rollo, 1983].

Prerequisites for the emergence of competitive interactions between *M. edulis* and *L. obtusata* do exist. Both species use macrophytes in general and *Fucus* in particular as a substrate for habitation. For *L. obtusata*, *F. vesiculosus* is the main substrate for habitation, feeding, and oviposition. In the case of *M. edulis*, it is just one of possible substrates for habitation; however, as our data show, even if only 5% of mussels inhabit *Fucus*, their biomass is already equivalent to that of *L. obtusata*. Competitive relationships between periwinkles and mussels can be indirect: in the case of a significant reduction in the area of the substrate suitable for habitation of *L. obtusata* recruits. Anyway, the presence of direct competition associated with *M. edulis* release of some biologically active substances (repellents or metabolites) seems to be more realistic. In this case, not only mussels inhabiting *Fucus*, but also molluscs attached to the underlying substrate may participate in the competition. This assumption is consistent with literature data: it has been shown, in particular, that mussels are capable of displacing both other molluscs and crustaceans from the substrate [Zolotnitsky, 2011].

Thus, the fourth component of the equation (1), *M. edulis* biomass, may evidence for the presence of interspecific competition or result from the occurrence of a common factor which both the density of *L. obtusata* recruits and the mussel biomass are correlated with. Additional studies are required to verify the assumptions made.

Notably, it would be logical to expect the presence of interspecific competitive interactions with a closely related cohabiting mollusc, *L. saxatilis*. However, we found no significant relationships between *L. saxatilis* abundance (biomass or abundance of different age groups) and the reproduction of the *L. obtusata* population. *L. saxatilis* abundance is not "included" in the final equation, either as an alternative to *M. edulis* biomass or in addition to the mussel abundance. Interestingly, the absence of a significant effect of *L. saxatilis* on the reproduction of the *L. obtusata* population does not exclude the possibility of the opposite effect, since interspecific competitive relationships are not necessarily symmetrical [Aguilera, Navarrete, 2012; Espinosa et al., 2006].

The reproduction of the mollusc population may be affected by parasites. Ten species of trematodes parasitize the White Sea *Littorina* representatives. As already mentioned, all the detected fluke species cause complete parasitic castration of molluscs [Galaktionov, 1993; Ganzha, Granovich, 2008; Granovitch, Sergiyevsky, 1990] and, therefore, to one degree or another affect the reproductive potential of a population. As shown in a number of cases, parasitic pressure leads to a pronounced decrease in the reproduction rate of the host population [Brown et al., 1988; Kohler, Wiley, 1992]. However, other cases are known – when the impact of parasites was not noticeable at the population level [Kube et al., 2006]. In our study, we found no significant relationship between abundance of recruits and the prevalence of infestation of the population ($R = +0.028$; $\alpha = 0.906$). Since the overall prevalence of infection was relatively low (4 to 15% in different years), this can be explained by a low infestation rate. Similarly, S. Sergievsky *et al.* [1997] recorded no effect of infestation on the reproduction rate of the *L. obtusata* population in the habitat we surveyed, although the prevalence of infestation in the period of their research (1982–1995) was significantly higher (20–60%). A. Granovich and A. Maximovich [2013] also did not register any effect of infection on the reproduction of the population; however, they reported a negative correlation between the host population density in the current year and the prevalence of trematode infection in the previous year mediated by the death of infected middle-aged individuals. In addition, a positive relationship was revealed between the prevalence of trematode infection in the previous year and abundance of *L. obtusata* aged one year in the current year. The latter result is in agreement with our observations on the occurrence of intraspecific competition between adult and juvenile periwinkles [Kozminsky, 2013, 2017, 2020; this study]. Most likely, the positive correlation found by the abovementioned authors is explained by the release of additional resources (a brown alga *F. vesiculosus*) when adult infected individuals die: this mediates survival of more juveniles.

**Conclusion.** Most of the studied variables were excluded from the analysis due to their low relevance or strong correlation with other variables. Apparently, a set of variables selected for multiple regression analysis or included in the final dependence (1) is not random: all of them reflect habitat conditions of molluscs (biotic and abiotic ones) and can be somehow associated with the reproduction rate of *Littorina obtusata* population. Specifically, *Fucus vesiculosus* biomass evidences for high abundance of the key resource limiting *L. obtusata* population size. The density of molluscs aged two years and older characterizes the rate of intraspecific competition between recruits and large individuals. A bivalve *Mytilus edulis* is one of the most common littoral species using *Fucus*, the same as the periwinkles do, as a substrate for habitation; due to it, interspecific competition is possible between them. Four climate variables ($H_{VII}$, $DS_{V–IX}$, $NAO_{JUL}$, and $NAO_{ASO}$) feature habitat conditions for juveniles during their first year of life. Out of them, the key role is played by the amount of precipitation which is involved in the final regression equation (1) and characterizes level of desalination of the surface layer of seawater.

The obtained equation (1) has a clear biological meaning. It shows as follows: during the study period, the reproduction of the *L. obtusata* population was governed by both intrapopulation factors and environmental factors (biotic and abiotic ones). Obviously, the reproduction of the *L. obtusata* population should be affected by a significantly larger number of factors than we revealed during the study. The level of effect and the set of factors may change with shifts in conditions of the population's existence: other factors may come to the fore.

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# ФАКТОРЫ, ВЛИЯЮЩИЕ НА ВОСПРОИЗВОДСТВО ПОПУЛЯЦИИ МОЛЛЮСКОВ *LITTORINA OBTUSATA* (GASTROPODA: LITTORINIDAE) В БЕЛОМ МОРЕ

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Изучение факторов, влияющих на изменения численности популяций, необходимо для понимания функционирования природных экосистем и планирования мероприятий по охране и менеджменту окружающей среды. Важным компонентом литоральных экосистем морей Северного полушария являются моллюски рода *Littorina*, однако факторы, определяющие динамику их численности, исследованы недостаточно. В настоящей работе представлены данные, полученные в ходе наблюдений за популяционной динамикой *Littorina obtusata* с 2001 по 2020 г. В этот период отмечены квазициклические изменения плотности популяции литторин вокруг среднего уровня, составляющего около 2,6 тыс. экз.·м$^{-2}$. Проанализировано 67 переменных, характеризующих состояние изученной популяции моллюсков и воздействие на неё ключевых биотических и экологических факторов. Показано, что изменения плотности популяции на 83 % обусловлены флуктуациями численности сеголеток. Множественный регрессионный анализ продемонстрировал, что уровень воспроизводства популяции *L. obtusata* на 78 % определялся флуктуациями четырёх переменных — плотности особей в возрасте двух лет и старше, биомассы водорослей *Fucus vesiculosus*, количества осадков в июле и биомассы двустворок *Mytilus edulis*. Первая переменная отражает уровень внутривидовой конкуренции, вторая — способность данного местообитания к поддержанию популяции моллюсков определённой численности, а третья — воздействие факторов окружающей среды. Наличие связи между уровнем воспроизводства популяции литторин и биомассой двустворок может быть объяснено либо существованием некоего общего фактора, с которым коррелированы обе переменные, либо наличием межвидовых взаимодействий между *M. edulis* и *L. obtusata*.

**Ключевые слова:** *Littorina obtusata*, численность популяции, флуктуации численности, биотические и абиотические факторы, внутривидовая конкуренция, межвидовая конкуренция, ёмкость местообитания