Effects of environmental and biotic factors on the fluctuations of abundance of *Littorina obtusata* (Gastropoda: Littorinidae)

Eugene V. Kozminsky

Abstract To explain periodic fluctuations in abundance of an intertidal flat periwinkle *Littorina obtusata,* we tested the potential impacts of several key environmental and biotic factors on the population density of this mollusc. The analysis showed that 79% of density variation was due to the changes of the recruitment of the periwinkles and likely caused by intraspecific competition for resources (algae *Fucus vesiculosus*) between the recruits and the older molluscs under the conditions of depleted habitat capacity. The cyclical changes in *L. obtusata* density result from the alternating periods of high and low recruitment. High recruitment is observed when the abundance of mature periwinkles is relatively low and enough resources are available to insure high survival of the recruits. The duration of high recruitment periods (approximately 3 years) is determined by the maturation time of the periwinkles. As the recruits mature, the density of adult periwinkles increases and the subsequent recruitment decreases. The duration of the low recruitment phases (an average of 3–4 years) appear linked to the longevity of mature *L. obtusata*.

E. V. Kozminsky (✉)
White Sea Biological Station, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034 Saint-Petersburg, Russia
e-mail: ekozminsky@gmail.com

As the adults age and die out, their density declines and the release of resources leads to an increase of recruitment heralding the beginning of the next cycle.

Introduction

Periodic fluctuations of population size have been found in various animals including mammals, birds, insects, and molluscs (MacLulich, 1937; Elton, 1942; Baltensweiler, 1964; Lack, 1966; Bachelet, 1986; Maximovich & Gerasimova, 2004). Population cycles can be related to temporal variation of food abundance, exposure to predators and parasites, intraspecific competition or genetic heterogeneity of the population (Hudson et al., 1998; Sinclair et al., 2003; Högstedt et al., 2005). However, in many cases, the causes of population cycles are not yet established and the underlying mechanisms remain obscure. In particular, there is no consensus on the existence of the feedback mechanisms of population size regulation. It is commonly accepted that population size is a result of the combination of random fluctuations and actions of regulatory mechanisms (Haldane, 1953; Nicholson, 1958; Zahvatkin, 2001). Proponents of an alternative point of view assert that the population size is limited

by multiple random factors making the feedback regulation unnecessary (Andrewartha & Birch, 1954). A study of factors causing cyclical changes in population size is necessary to identify the common patterns and underlying mechanisms. This knowledge is important for a deeper understanding of the functioning of natural ecosystems and as a prerequisite for environmental management (evaluation of a sustainable population size for a given amount of food resources or predator exposure levels, assessment of the transmission efficiency of parasites depending on the size of the host population and the likelihood of epizootics, etc.). In this regard, it is essential that relevant research cover the widest possible range of biological objects.

The population dynamics of two species of molluscs, *Littorina obtusata* (Linnaeus, 1758) (flat periwinkle) and *L. saxatilis* (Olivi, 1792) (rough periwinkle), have been extensively studied from 1982 to 1995 during a long-term monitoring survey at the White Sea Biological Station of the Zoological Institute (Sergievsky et al., 1997). The periwinkles are small (about 10 mm in diameter) grazing intertidal gastropods. Both species have largely overlapping spatial distributions in the intertidal zone. *L. obtusata* prefers the middle and lower intertidal levels, while *L. saxatilis* is common in the upper, middle, and lower intertidal zone. Both species are the first intermediate hosts for several species of trematodes (Galaktionov & Dobrovolsky, 1984; Sergievsky, 1985; Granovitch et al., 2000), including those causing severe disease in marine waterfowl (Kulatchkova, 1960, 1979). One of the most interesting results obtained in these earlier long-term studies was the discovery of cyclical changes in abundance of *L. obtusata*, associated with recruitment fluctuations (Sergievsky et al., 1997). Infection by trematodes leads to a full parasitic castration of periwinkles (Granovitch & Sergievsky, 1990; Galaktionov, 1993; Ganzha & Granovitch, 2008) and, consequently, negatively affects reproduction in the host population. In some cases, the influence of parasites on host fecundity may cause the periodic fluctuations of population size (Hudson et al., 1998). Therefore, it can be hypothesized that the cyclical changes of recruitment in *L. obtusata* are driven by variations in infection prevalence. However, the link between the population dynamics and the level of trematode infection has not been established (Sergievsky et al., 1997), and causes of the cyclical

changes in population size of *L. obtusata* remain unclear.

The present paper is based on data of the monitoring survey of the same population carried out from 2001 to 2010. During this period, the change in the abundance of *L. obtusata* was also observed that appear to continue the periodical cycles described in earlier studies (Sergievsky et al., 1997). The aims of the present study were (i) to identify factors affecting population size of *L. obtusata* and hence the causes for the density fluctuations in 2001–2010 and (ii) to develop hypotheses explaining cyclical changes in abundance of this species. Specifically, I tested the hypotheses that the cyclical changes in the population density of flat periwinkles may be due to the impact of the environmental factors (such as temperature, rainfall and salinity) alone or in combination with the biotic factors (such as algal biomass, the parasitic pressure, and intra- and interspecific competition). Biotic factors (i.e., food resource availability and intraspecific competition) have emerged as the main factors affecting the abundance cycles of the flat periwinkle populations.

Materials and methods

Study site

The study site is located on the western spit of Yuzhnaja Inlet at Ryashkov Island (67°00′09″N, 32°34′42″E; Kandalaksha Nature Reserve). The island lies at the head of Kandalaksha Bay about 14 km from Kandalaksha. Yuzhnaja Inlet is oriented toward the mouth of the bay. The nearby waters are shallow (maximum depth less than 10 m) and are separated from the open sea by a number of islands, which leads to a moderate level of wave exposure. The inner part of Kandalaksha Bay is brackish due to the freshwater input from the rivers Niva, Kovda, and some smaller rivers.

The study is based on the regular surveys of *L. obtusata* population from 2001 to 2010. The surveyed area lies between the hydrographic datum and a large intertidal pool, lined with fine sand and scattered with individual stones. The inclination of the shore in the vicinity of the transect is approximately 1.6–1.7 degrees, the spring high tide level is about 2.9 m. The upper part of the transect becomes

exposed about 2 h before low tide and is submerged again 2 h after low tide. The sediment consists mainly of small and medium-sized gravel mixed with moderately silted sand. The intertidal zone is covered with stones of various sizes and up to 1.5 m boulders. Most of the area (to a distance of 20 m from the datum) is covered with the brown algae *Fucus vesiculosus* (Linnaeus, 1753). Near the datum this species co-dominates with another brown algae *Ascophyllum nodosum* (Le Jolis, 1863). The invertebrate fauna is typical for the White Sea rocky intertidal zone (Naumov & Olenev, 1981), with occasional occurrence of some common soft-bottom intertidal species such as the molluscs *Macoma balthica* (Linnaeus, 1758) and *Hydrobia ulvae* (Pennant, 1777) and the holothurian *Chiridota laevis* (Fabricius, 1780).

Environmental data

Data on air temperature and rainfall during the research period, collected at the weather station "Kandalaksha" (No. 22217), were taken from the website of the Russian Research Institute of Hydrometeorological Information-World Data Center (RIHMI-WDC, http://meteo.ru/climate/sp_clim.php); data on air and sea surface water temperature, as well as salinity in the Yuzhnaja Inlet at Ryashkov Island in 2007–2009 were taken from the publications of Khaitov (2008, 2009, 2010). Correlation analysis showed that the temperature data of the weather station "Kandalaksha" were a good estimate of air temperature in the Yuzhnaja Inlet (Spearman rank correlation coefficient $R_s \geq 0.85$, $P \ll 0.001$, in different years) and an acceptable estimate of the sea surface water temperature ($R_s \geq 0.59$, $P \ll 0.001$, in different years).

Three indicators were used to assess the impact of thermal conditions on the reproduction of the population of the littorines: the sum of average daily air temperatures during the period from May 25 to September 4, the number of frosts and the number of days with temperatures above 22°C during the period of embryonic development of the littorines (from May 25 to June 25). The latter two parameters were calculated using only the dates when the daily minimum or maximum temperature coincided with the period of low tide (±2 h from the lowest water) based on the data from the weather station "Kandalaksha". Given that the temperature in Kandalaksha

is on average 0.5°C higher than on Ryashkov Island, all the data were corrected for that value.

To estimate the amount of precipitation that could affect the salinity, we used two variables calculated for each year of observations: the total precipitation from November 1 of the preceding year to September 4 of the given year, and from May 25 to September 4 of the given year. The first period corresponds to the amount of precipitation in the form of snow during the cold season (November–March) and in the form of rain during the warm season (April–September). It determines the annual rate of freshening (and thus, the average salinity) in the littorine habitat in spring and summer. The second period corresponds to the amount of precipitation directly during egg-laying, hatching, and development of new recruits.

Sampling

Sampling was carried out once a year, between August 10 and September 4 in 2001–2010. Samples were collected quantitatively from 0.025 m² plots (0.16 m × 0.16 m). The top 0.5–1.5 cm layer of sediment and all the seaweeds were collected from the plots. The plots were arranged in groups of three along the transect perpendicular to the shore. The groups of plots were located at a distance of 0, 5, 10, 15, 20, and 25 m from the mean low water level. The plots within each group were arranged perpendicular to the transect. To cover the range of possible substrates more accurately, in different years I sampled 3–7 randomly chosen plots from the surface of the medium and large stones along the transect.

The collected samples (from 20 to 29 plots in different years) were transferred to the laboratory where they were rinsed in fresh water, sieved (0.6 mm mesh size), and sorted. The samples from the same level on a transect were considered replicates and were processed separately. In each sample, wet weight of fucoid algae (separately for *F. vesiculosus* and *A. nodosum*) to the nearest 0.5 g was determined. Filamentous algae (approximately 3/4 of the biomass was accounted for by *Cladophora* sp. and 1/4 by *Stictyosiphon* sp.) were weighed to the nearest 0.1 g and molluscs were weighed as follows: *L. obtusata* and *L. saxatilis* to the nearest 1 mg, *Mytilus edulis* to the nearest 0.5 g. The littorines were counted.

Age of *L. obtusata* was determined individually and the maximum shell diameter was measured to the

nearest 0.1 mm. The periwinkles were dissected to determine their sex and the presence of trematode infection. Age of molluscs was determined by annual growth interruption lines ("annual rings"), with regard to the shell growth dynamics and the degree of erosion (Kozminsky, 2005, 2006). We used the following age notation: new recruits (individuals hatched during the current year)—0+, "molluscs aged 1 year"/"1-year-old snails" (hatched during the previous year)—1+, "molluscs aged 2 years"/"2-year-old snails" (hatched during the penultimate year)—2+, etc. When combining age groups we used terms: molluscs aged 1+ and older for individuals aged 1+, 2+, etc. to the oldest age group (8+) inclusively; molluscs aged 3+ and older for individuals aged 3+, 4+, etc. to the oldest age group (8+) inclusively.

In the White Sea, *L. obtusata* is the first intermediate host for several species of trematodes (Galaktionov & Dobrovolsky, 1984; Sergievsky, 1985; Granovitch et al., 2000). All of them cause full parasitic castration (Granovitch & Sergievsky, 1990; Galaktionov, 1993; Ganzha & Granovitch, 2008) and, therefore, affect the reproduction of the host population. For the purposes of this study, we used the prevalence of infection by all trematodes as a measure of the entire parasite pressure on the reproduction of periwinkles.

Over the years, an average of only 0.4% of *L. obtusata* were found in the additional plots from the surface of medium and large stones along the transect. So, the data from these plots were excluded from analyses. In the case of *A. nodosum*, which occurs only at levels of 0 and 5 m, the data from the plots from the two lower levels of the transect were used in the calculation of the biomass.

Statistics

Population densities were compared between years using the Kolmogorov–Smirnov test (Lloyd & Lederman, 1989). Spearman rank correlation coefficient R_s was chosen as a measure of association between the variables (Hettmansperger, 1987), because variable distribution differed from normal for several tested variables. The proportion of population variability of recruits explained by various factors was estimated using the coefficient of determination (R_s^2). To evaluate the relationships between variables that involve some delay, we used a distributed lag analysis
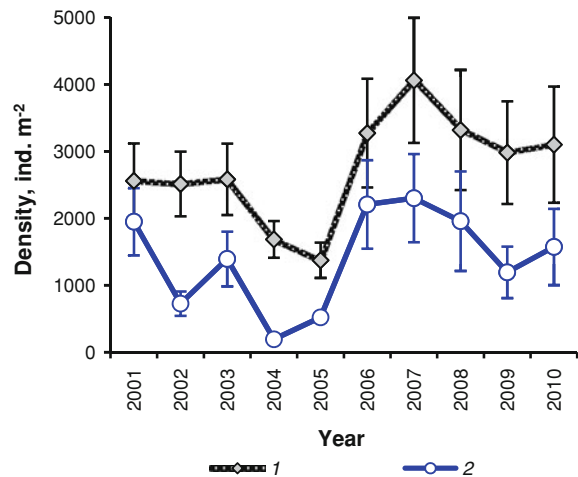

Fig. 1 Long-term variation of the overall population density of *L. obtusata* (*1*) and the density of recruits (*2*). *Error bars* are standard errors of the means

(Judge et al., 1985) and cross-correlation function (R_{cc}; Box & Jenkins, 1976).

Results

During the study, there was a wave-like change in population density of *L. obtusata* (Fig. 1, variable 1). At the beginning (2001–2003) and at the end of the study period (2008–2010), the population density was almost constant. Significant changes of density (Kolmogorov–Smirnov test, $P < 0.025$) occurred in 2004–2007.

We found a highly significant relationship between the total population density and density of recruits[1] of *L. obtusata* ($R_s = 0.89$, $t(8) = 5.548$; $P < 0.001$). Therefore, 79% of the observed density variation was explained by changes in the number of recruits (Fig. 1, variable 2).

No association was detected between the studied abiotic environmental factors and recruitment of *L. obtusata* (Table 1, factors 1–5).

The correlation between the sum of average daily air temperatures in summer and density of recruits was not significant. No lagged relationship between the temperature and the number of recruits was revealed since there were no significant regression coefficients

---

[1] Hereafter, "the density of recruits", "the number of recruits," "recruitment" are used as synonyms.

Table 1 Spearman rank correlation coefficients between density of *L. obtusata* recruits and various factors

	Factors													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*
R_s	−0.33	0.32	0.48	0.30	−0.08	−0.43	0.32	−0.54	0.36	−0.47	0.07	−0.26	−0.72	−0.36
$t(N-2)$	−1.00	0.97	1.56	0.88	−0.22	−1.35	0.96	−1.81	1.08	−1.49	0.19	−0.76	−2.95	−1.08
P-level	0.347	0.361	0.159	0.405	0.829	0.214	0.365	0.108	0.310	0.174	0.855	0.467	0.019	0.310

1 sum of average daily air temperatures from 25.V to 4.IX; *2* and *3* number of days with temperatures above 22°C and the number of frosts during low tide in the period of embryonic development of *L. obtusata*, respectively; *4* and *5* total precipitation from 1.XI of the previous year to 4.IX and from 25.V to 4.IX, respectively; *6* biomass of *A. nodosum*; *7* biomass of filamentous green algae; *8* biomass of *M. edulis*; *9* density of *L. saxatilis*; *10* total infection prevalence; *11* biomass of *F. vesiculosus*; *12* number of adult (age 3+ and older) females; *13* biomass of littorines aged 1+ and older; *14* number of mature (age 3+ and older) littorines. R_s, Spearman rank correlation coefficient; $t(N-2)$, Student's *t* test, *P* value, the level of significance

in the distributed lag analysis ($P > 0.05$). Relationships between the presence of frosts or high temperatures (22°C and more) at low tide and the number of recruits were not detected either.

No association was detected between the total precipitation from preceding November 1 to September 4 of the given year and the density of recruits. There was also no significant correlation between the precipitation during the summer and the density of recruits. In both cases, no delayed relationship with the density of recruits has been identified, as the regression coefficients for all possible lags were not significant ($P > 0.05$).

The number of recruits was not associated with biomass of *A. nodosum*, green filamentous algae, *M. edulis*, population density of *L. saxatilis* or the prevalence of trematode infestation of the mature females of *L. obtusata*. The correlation coefficients in all cases were not significant (Table 1, factors 6–10). Distributed lag analysis revealed no delayed relationship between these variables and the number of recruits ($P > 0.05$).

We found that recruitment of *L. obtusata* was associated with *F. vesiculosus* biomass changes. The change in the number of recruits was 1 year ahead of the biomass change of *F. vesiculosus* (Fig. 2, variables 1 and 3). Spearman correlation coefficient between those variables was close to zero (Table 1, factor 11). However, the distributed lag analysis revealed a lagged relationship between the variables: the regression coefficient corresponding to the lag "1 year" was the highest and significant ($P = 0.040$).The highest value of cross-correlation function also corresponded to this lag ($R_{cc} = 0.73$, $P < 0.05$). It is worth noting that the number of 1-year-old snails changed synchronously with the *Fucus* biomass ($R_s = 0.71$, $t = 2.81$; $P = 0.023$), while the density of 2-year-old snails followed it with a 1-year lag ($R_{cc} = 0.73$; $P < 0.05$), and the density of 3-year-old snails with a 2-year lag ($R_{cc} = 0.71$; $P < 0.05$), etc.

The change of the number of recruits of *L. obtusata* was not related to the changes in the number of adult females (age 3+ and older; Table 1, factor 12). In fact, the relationship between the variables was almost in antiphase, and, in the distributed lag analysis, the regression coefficient corresponding to the lag "3 years" was the highest ($P = 0.054$).

It was found that the density of recruits and biomass of littorines aged 1+ and older were almost in

Fig. 2 Long-term variation of the number of recruits (*1* left *y* axis, *left scale*) and mature individuals (*2* left *y* axis, *right scale*) of *L. obtusata* and *F. vesiculosus* biomass (*3* right *y* axis). *Error bars* are standard errors of the means
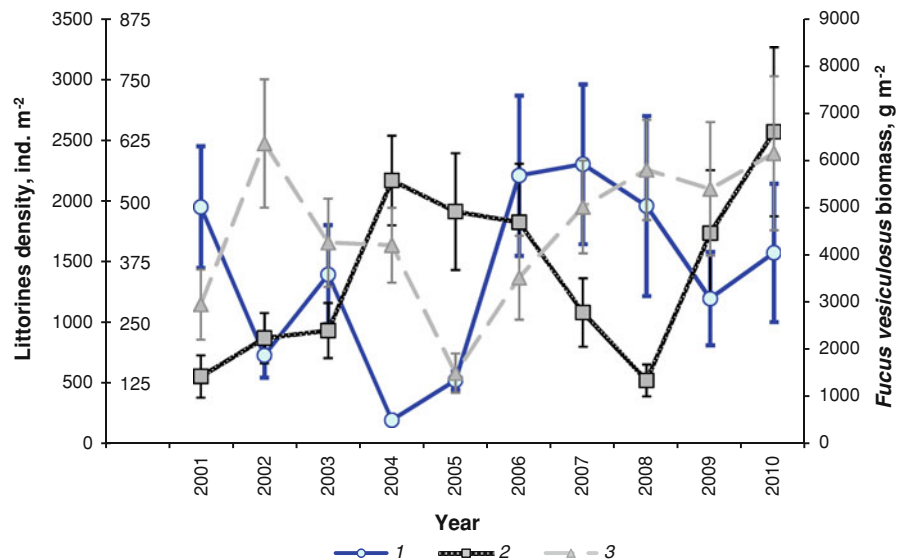
antiphase (Table 1, factor 13), while no similar relationship with the number of snails aged 1+ and older was identified. For the latter group, Spearman correlation coefficient, the values of the cross-correlation function and the regression coefficients in the analysis of distributed lags were not significant. At the same time, the relationship between the number of recruits and mature individuals (aged 3+ and older) was close to antiphase (Fig. 2, variables 1 and 2). The correlation coefficient was negative, but nonsignificant (Table 1, factor 14). Distributed lag analysis also indicated the presence of lagged relationships between the variables: the regression coefficient corresponding to the lag "3 years" was the largest and approaching significance ($P = 0.063$).

Changes in the number of recruits were a year ahead of the density of 1-year-old snails (the cross-correlation function at lag "1 year" $R_{cc} = 0.78$; $P < 0.05$), 2 years ahead of density of 2-year-old snails ($R_{cc} = 0.58$ lag in the "2 years"; $P = 0.085$) and 3 years ahead of 3-year-old snails ($R_{cc} = 0.69$ for lag "3 years"; $P = 0.063$). In addition, in the latter case, the regression coefficient for lag "3 years" was the highest and significant as shown by the distributed lag analysis ($P = 0.027$).

Discussion

Density of the studied population of flat periwinkles undergoes prominent multiannual cyclical fluctuations as

evidenced by long-term studies. In the studied population of *L. obtusata*, the density maxima were registered in 1985 and 1992 (Sergievsky et al., 1997), and in 2007 (this study). We suggest that there is a 7–8 year period in the fluctuations, taking into account that there were no data on the abundance of littorines from 1996 to 2000. The changes in population density revealed in this study may be a fragment of one of the cycles.

By analyzing changes in littorine population density, Sergievsky et al. (1997) concluded that they can be linked to recruitment level. Consistent with this conclusion, we found that 79% of density variation in the overall population size was due to the changes in the number of recruits. Our data also demonstrate that the observed recruitment fluctuations in *L. obtusata* were caused by intraspecific competition for resources in a habitat of limited capacity. Indeed, the number of recruits varied in antiphase with the biomass of molluscs of other ages. This indicates that the level of recruitment is determined by the presence of unexploited resources and that intraspecific competition takes place. At the same time, no antiphase relationships between the number of recruits and molluscs aged 1+ and older were observed. An antiphase relationship of the number of recruits with their biomass, but not with density of snails aged 1+ and older seems contradictory. However, this may be explained by the fact that the main contributors to the biomass were the mature individuals (ages 3+ and older) and their density, in turn, varied in antiphase with the number of recruits.

As expected, fluctuations in the number of recruits were a year ahead of the respective changes in the

density of molluscs aged 1+, 2 years ahead—for snails aged 2+, 3 years ahead—for age 3+, etc. Consequently, the presence of the antiphase relationship between the number of recruits and molluscs aged 3+ (and the almost antiphase relationship with mature individuals in general) is a natural consequence of the demographic processes in populations of *L. obtusata*. At the same time, this phenomenon can be seen as a feedback mechanism of recruitment regulation.

Our results indicate that significant demographic events (changes in the numbers of recruits and mature individuals) occur in the context of *F. vesiculosus* biomass dynamics (Fig. 2). *F. vesiculosus* and its microfouling are the main sources of food and a substrate for *L. obtusata* (Kuznetzov, 1960; Beskupskaja, 1963; Matveeva, 1974; Barker & Chapman, 1990; Reid, 1996). It is therefore logical to assume that littorines compete for this resource and, consequently, the population abundance of *L. obtusata* in this locality is limited by the resource capacity of *F. vesiculosus*. Intraspecific competition for food is common in littorines. For instance, it has been reported in *Littorina plena* and *Littorina unifasciata* (Branch & Branch, 1981; Chow, 1989). Fluctuations in population size driven by intraspecific competition are also found in bivalve molluscs. Thus, Bachelet (1986) found that variation in the number of settlers due to intraspecific competition with older individuals was the main cause of temporal variation of *M. balthica* density. When studying the population dynamics of bivalves in the Chupa Inlet of the White Sea, Maximovich and Gerasimova (2004) found that a few generations dominated the assemblages of *M. edulis*, *Mya arenaria* and *M. balthica* during several consecutive years. These authors also attributed this phenomenon to the intraspecific competition between adults and recruits, which prevented spat settlement and/or survival of the recruits. While the increase of density of mature individuals of *L. obtusata* influences the recruitment level, our data are insufficient to determine the possible mechanisms of this effect, which may include decreased fertility of snails, failure of individuals to participate in reproduction, or increased recruit mortality when resources decline. Further research is needed to answer this question.

Based on the findings of the present study, the following scenario of the dynamics of changes in the number of recruits, mature individuals and biomass of *F. vesiculosus* can be proposed. In 2001, the density of mature individuals was small, while the biomass of *F. vesiculosus* was moderate, so the level of recruitment was quite high. In 2002–2004, the biomass of *Fucus* decreased and the density of mature individuals increased, leading to a reduced recruitment. In 2005, *Fucus* biomass sharply declined, but the number of mature snails started to decrease, and, therefore, the recruitment increased. In 2006–2007, *Fucus* biomass increased, and the number of mature individuals continued to decline. This was associated with a considerable increase in the number of recruits. In 2008, the recruitment decreased, despite increasing *Fucus* biomass and declining number of mature individuals. This can be explained by the fact that the main contribution to the reproduction of the population at this time was made the numerically small cohort of snails hatched in 2004–2005. In 2009, the *Fucus* biomass changed little, but the density of mature individuals began to increase due to high recruitment of littorines in 2006. Consequently, recruitment continued to decline. In 2010, biomass of *F. vesiculosus* slightly increased, so, despite the increase in density of mature individuals, recruitment also slightly increased.

Notable fluctuations in the number of recruits were observed against the background of a general decline of recruitment in 2001–2004. These can be explained based on the data obtained by Kuznetzov (1946). He found that *L. obtusata* requires 0.039 g of food per 1 g of body weight per day. In the surveyed locality, the average biomass of recruits and the snails aged 1 year and older was 0.6 and 83.1 g m^{-2}, respectively. Accordingly, the food requirements of individuals in these groups were different: 1,400 recruits consume as much food as four individuals of medium size (shell diameter of 7 mm and weighing 150 mg). However, four adult individuals correspond to only 0.3% on average of the total number of periwinkles aged 1 year and older from an area of 1 m^2. Therefore, even minor fluctuations in the demographic composition of this part of the population were sufficient to cause significant changes in the recruitment.

The proposed mechanism may also explain the above-mentioned cyclical changes of population density of *L. obtusata* with a period of 7–8 years. It can be based on alternating periods of high and low levels of recruitment in a habitat of limited capacity and competition for resources (*F. vesiculosus*), otherwise, the density of the population would grow indefinitely. The observed 7–8 years periodicity is

related to the life cycle characteristics of *L. obtusata*. Analysis of our data (Figs. 1, 2), and the data of Sergievsky et al. (1997) shows that high recruitment periods lasted about 3 years. We suggest that during these periods, the density of mature individuals can be relatively low. The periwinkles hatched at the beginning of this period reach maturity when it ends. As the density of mature snails increases, the level of recruitment starts to decline. This process continues during the two subsequent years. The longevity of most *L. obtusata* does not exceed 5 or 6 years (Kuznetzov, 1960; Matveeva, 1974; Kozminsky, 2006). Consequently, mature individuals live an average of 3–4 years. So, by the time the periwinkles that have hatched at the end of the high recruitment period reach sexual maturity, the number of individuals hatched in the beginning already starts to decline. The gradual release of resources can lead to an increase of recruitment and to the next density peak.

Obviously, the regular frequency of density changes can be observed only under ideal conditions. In practice, the changes in *F. vesiculosus* biomass, and the impact of other factors on the density of littorines can lead to deviations from the ideal cycle. Therefore, in reality, quasi-cycles rather than cycles are observed. If my hypothesis is correct, the next peak of reproduction can be expected around 2014–2015, which would verify the assumptions I made. It is also possible that cyclical fluctuations of density of the littorines may be maintained by the periodic variation of the *Fucus* biomass. For instance, the cycle may be triggered by an abrupt decline of *F. vesiculosus* biomass due to winter ice scouring.

Although *L. obtusata* prefer living on the seaweed *F. vesiculosus* (Kuznetzov, 1960; Beskupskaja, 1963; Matveeva, 1974; Barker & Chapman, 1990; Reid, 1996), they can also use *A. nodosum* as a food source and the substrate (Pavia & Toth, 2000; Toth & Pavia, 2000). Younger *L. obtusata* (about 4 mm shell diameter) can also be cultivated using green filamentous algae for food, although they grow slower than average (Kozminsky, unpublished data). Thus, these alternative substrates can be used by periwinkles but likely much less efficiently than *F. vesiculosus*, which explains the lack of correlation between the density of *L. obtusata* recruits and the biomass of *A. nodosum* or filamentous algae.

Interspecific competition for food can also occur between different species of littorines (Yamada & Mansour, 1987). In the studied habitat, *L. saxatilis* is a

likely potential competitor of *L. obtusata* because a considerable proportion of its population (about 52% of individuals) occurs on *F. vesiculosus*. However, due to its wide habitat preferences, *L. saxatilis* can also occupy other substrates when the abundance of *F. vesiculosus* decreases. This can alleviate the competition and may explain the lack of connection between the density of *L. saxatilis* and that of *L. obtusata* recruits. Similarly, no association between the number of recruits of *L. obtusata* and biomass of mussels was found, although the correlation coefficient was quite high (Table 1, factor 8) because both variables were correlated with changes in biomass of *F. vesiculosus*. The negative value of the correlation coefficient is explained by the fact that the changes in the number of *L. obtusata* recruits were ahead of *F. vesiculosus* biomass dynamics and *M. edulis* biomass supervened it.

The White Sea periwinkles host ten species of trematodes, and all of them are able to cause full parasitic castration (Granovitch & Sergievsky, 1990; Galaktionov, 1993; Ganzha & Granovitch 2008) and may therefore limit the reproductive potential of littorine population. In this study, no correlation between the trematode prevalence and host recruitment was found suggesting that the parasites did not limit the host recruitment. Similar findings were reported in *Hydrobia ventrosa* populations infected by trematodes (Kube et al., 2006), while in other host–parasite systems the parasite pressure was shown to limit the recruitment of the host population (Brown et al., 1988; Kohler & Wiley, 1992).

The total rainfall from the preceding November 1 to September 4 of the current year may be used as an indicator of salinity in different years, because the amount of precipitation determines the degree of freshening. The available data on salinity in the Yuzhnaja inlet at Ryashkov Island are limited to 2007–2009 (Khaitov, 2008, 2009, 2010). The average salinity in the summer of 2007, 2008, and 2009 was 18.8, 19.9, and 20.2 ppt, and the amount of rainfall—565, 531, and 525 mm, respectively. This confirms the link between the level of freshening and the amount of precipitation. As in 2001–2006, rainfall did not exceed 510 mm, there is no reason to believe that salinity conditions in these years had been worse. Accordingly, the observed fluctuations in the number of recruits are likely not associated with changes in the average salinity.

Notably, none of the analyzed environmental variables (including temperature, salinity and rainfall)

affected the population abundance and the level of recruitment of the periwinkles in this study. This is likely to reflect the relatively moderate fluctuation of the environmental conditions during this study rather than insensitivity of the periwinkles to these factors. Thus, temperature was shown to affect the population size of *L. plena* (Chow, 1989). Freezing at low tide causes massive destruction of embryos in clutches of *L. obtusata* (Kozminsky, unpublished data), and the temperature over 22°C leads to an increased death rate of juveniles and the frequency of embryonic malformations (Kozminsky et al., 2008). Abrupt changes in salinity can also result in massive loss of both recruits and adult littorines. For example, in the second half of June 1966, the ice from the open part of the White Sea basin scoured the entire Kandalaksha Bay. As a result of ice melting, the salinity in some areas dropped to extremely low values of 0.3 ppt which is below the tolerance levels of the recruits of *L. obtusata* (Rusanova & Khlebovich, 1967).

Conclusions

As a corollary, our data indicate the existence of the feedback regulation of population size of *L. obtusata*, which is consistent with the population regulation by density-dependent mechanisms (Haldane, 1953; Nicholson, 1958; Zahvatkin, 2001) that assume that population size is determined by the random fluctuations of abundance and feedback mechanisms. The driving force of this regulation in *L. obtusata* population is likely intraspecific competition for a limited resource—*F. vesiculosus*. Several other factors (such as the level of infection, competition with *L. saxatilis*, or periodical extremes of temperature and salinity) can also limit the population size of *L. obtusata* under certain conditions although their role appeared to be negligible during the period of the present study.

References

Andrewartha, H. G. & L. C. Birch, 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Bachelet, G., 1986. Recruitment and year-to-year variability in a population of *Macoma balthica* (L.). Hydrobiologia 142: 233–248.

Baltensweiler, W., 1964. *Zeiraphera griseana* Hubner (Lepidoptera: Tortricidae) in the European Alps. A contribution to the problem of cycles. Canadian Entomologist 96: 762–800.

Barker, K. M. & A. R. O. Chapman, 1990. Feeding preferences of periwinkles among four species of *Fucus*. Marine Biology 106: 113–118.

Beskupskaja, T. P., 1963. Nutrition of some common littoral invertebrates in the White Sea. Proceedings of the Kandalaksha Reserve 4: 114–135 (in Russian).

Box, G. E. P. & G. M. Jenkins, 1976. Time Series Analysis: Forecasting and Control. Holden-Day, San Francisco.

Branch, G. M. & M. L. Branch, 1981. Experimental analysis of intraspecific composition in an intertidal gastropod, *Littorina unifasciata*. Australian Journal of Marine and Freshwater Research 32: 573–589.

Brown, K. M., B. K. Leathers & D. J. Minchella, 1988. Trematode prevalence and the population dynamic of freshwater pond snails. American Midland Naturalist 120: 289–300.

Chow, V., 1989. Intraspecific competition in a fluctuating population of *Littorina plena* Gould (Gastropoda: Prosobranchia). Journal of Experimental Marine Biology and Ecology 130: 147–165.

Elton, Ch., 1942. Voles, Mice and Lemmings: Problems in Population Dynamics. University Press, Oxford.

Galaktionov, K. V., 1993. The Life Cycles of Trematodes as the Components of Ecosystems. Kola Scientific Centre, Apatity (in Russian).

Galaktionov, K. V. & A. A. Dobrovolsky, 1984. An experience of population analysis of the trematode life cycles using microphallids of "pygmaeus" group (Trematoda: Microphallidae) as an example. In Polyansky, Yu. I. (ed.), Ecologo-parasitological Investigations of the Northern Seas. Kola branch of AS USSR, Apatity: 8–41 (in Russian).

Ganzha, E. V. & A. I. Granovitch, 2008. Modification of the structure of penial glands in males of the intertidal molluscs *Littorina saxatilis* and *L. obtusata* under the influence of the infestation by trematode parthenites. Parazitologia 42: 13–22 (in Russian).

Granovitch, A. I. & S. O. Sergievsky, 1990. Estimation of reproductive structure of *Littorina saxatilis* (Olivi)

(Gastropoda, Prosobranchia) populations in the White Sea. Zoologicheskij Zhurnal 69: 32–41 (in Russian).

Granovitch, A. I., S. O. Sergievsky & I. M. Sokolova, 2000. Spatial and temporal variation of trematode infestation in coexisting populations of intertidal gastropods *Littorina saxatilis* and *L. obtusata* in the White Sea. Diseases of Aquatic Organisms 41: 53–64.

Haldane, J. B. S., 1953. Animal populations and their regulation. New Biology 15: 9–24.

Hettmansperger, T. P., 1987. Statistical Inference Based on Ranks. Finances and Statistics, Moscow (in Russian).

Högstedt, G., S. Tarald & B. Arild, 2005. Period length in cyclical animal populations. Ecology 86: 373–378.

Hudson, P. J., A. P. Dobson & D. Newborn, 1998. Prevention of population cycles by parasite removal. Science 282: 2256–2258.

Judge, G. G., W. E. Griffith, R. C. Hill, H. Luetkepohl & T. S. Lee, 1985. The Theory and Practice of Econometrics. Wiley, New York.

Khaitov, V. M., 2008. Dynamics of salinity and temperature of seawater, Yuzhnaja inlet, Ryashkov Island, 31.05–20.08.2007. In Koryakin, A. S. (ed.), The Chronicle of Nature of the Kandalaksha Reserve for 2007, Vol. 1. Kandalaksha Reserve, Kandalaksha: 83–88.

Khaitov, V. M., 2009. Dynamics of salinity and temperature of seawater, Yuzhnaja inlet, Ryashkov Island, 23.05–20.08.2008. In Koryakin, A. S. (ed.), The Chronicle of Nature of the Kandalaksha Reserve for 2008, Vol. 1. Kandalaksha Reserve, Kandalaksha: 57–68.

Khaitov, V. M., 2010. Dynamics of salinity and temperature of seawater, Yuzhnaja inlet, Ryashkov Island, 09.06–23.08.2009. In Koryakin, A. S. (ed.), The Chronicle of Nature of the Kandalaksha Reserve for 2009, Vol. 1. Kandalaksha Reserve, Kandalaksha: 79–90.

Kohler, S. L. & M. J. Wiley, 1992. Parasite-induced collapse of populations of a dominant grazer in Michigan streams. Oikos 65: 443–449.

Kozminsky, E. V., 2005. Growth and the use of dimensions data for determination of individual age of *Littorina obtusata* (Gastropoda, Prosobranchia). In The study, Sustainable Use and Conservation of Natural Resources of the White Sea. Karelia, Petrozavodsk: 146–150 (in Russian).

Kozminsky, E. V., 2006. Determination of age in *Littorina obtusata* (Gastropoda, Prosobranchia). Zoologicheskij Zhurnal 85: 146–157 (in Russian).

Kozminsky, E. V., P. A. Lezin & M. V. Fokin, 2008. A methodology of studying the inheritance of shell color in molluscs of the genes *Littorina* (Gastropoda, Prosobranchia). Zoologicheskij Zhurnal 87: 614–619 (in Russian).

Kube, S., J. Kube & A. Bick, 2006. A loss of fecundity in a population of mudsnails *Hydrobia ventrosa* caused by larval trematodes does not measurably affect host population equilibrium level. Parasitology 132: 725–732.

Kulatchkova, V. G., 1960. The death of common eider chicks and its causes. Proceedings of the Kandalaksha Reserve 3: 91–116 (in Russian).

Kulatchkova, V. G., 1979. Helminths as a cause of death for common eider in the Kandalaksha Bay. In Kishinskiy, A. A. (ed.), Ecology and Morphology of Eiders in the USSR. Nauka, Moscow: 119–125 (in Russian).

Kuznetzov, V. V., 1946. Nutrition and growth of herbivorous marine invertebrate in the Eastern Murman. In Proceedings of the USSR Academy of Sciences, Biological series 4: 431–452 (in Russian).

Kuznetzov, V. V., 1960. White Sea and Biological Features of Its Flora and Fauna. AS USSR Publishing, Moscow (in Russian).

Lack, D. L., 1966. Population Studies of Birds. Clarendon Press, Oxford.

Lloyd, E. & W. Lederman, 1989. Handbook of Applicable Mathematics, Vol. I. Finances and Statistics, Moscow (in Russian).

MacLulich, D. A., 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). University of Toronto studies, Biological series 43: 1–136.

Matveeva, T. A., 1974. Ecology and life cycles of common gastropod species in the Barenz and the White Seas. In Byhovskiy, B. E. (ed.), Seasonal Phenomena in the Life of the White and the Barents Seas. Nauka, Leningrad: 65–190 (in Russian).

Maximovich, N. V. & A. V. Gerasimova, 2004. Long-term monitoring of intertidal beds of bivalve molluscs in the Chupa Inlet (White Sea). In Railkin, A. I. (ed.), Marine and Freshwater Biological Systems in North Karelia. Saint-Petersburg State University, Saint-Petersburg: 95–120.

Naumov, A. D. & A. V. Olenev, 1981. Zoological Excursions at the White Sea. Leningrad State University Press, Leningrad (in Russian).

Nicholson, A. J., 1958. Dynamics of insect populations. Annual Review of Entomology 3: 107–136.

Pavia, H. & G. B. Toth, 2000. Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. Ecology 81: 3212–3225.

Reid, D. G., 1996. Systematics and Evolution of *Littorina*. The Dorset Press, Dorchester.

Rusanova, M. N. & V. V. Khlebovich, 1967. The effect on the White Sea fauna of abnormal conditions in the 1965–1966 years. Okeanologiya 7: 164–167 (in Russian).

Sergievsky, S. O., 1985. Populational approach to the analysis of the periwinkle *Littorina obtusata* (L.) invasion with trematode parthenitae. Helmintologia 22: 5–14.

Sergievsky, S. O., A. I. Granovitch & I. M. Sokolova, 1997. Long-term studies of *Littorina obtusata* and *Littorina saxatilis* populations in the White Sea. Oceanologica Acta 20: 259–266.

Sinclair, A. R. E., D. Chitty, C. I. Stefan & C. J. Krebs, 2003. Mammal population cycles: evidence for intrinsic differences during snowshoe hare cycles. Canadian Journal of Zoology 81: 216–220.

Toth, G. B. & H. Pavia, 2000. Water-borne cues induce chemical defense in a marine alga (*Ascophyllum nodosum*). Proceedings of the National Academy of Sciences of the USA 97: 14418–14420.

Yamada, S. B. & R. A. Mansour, 1987. Growth inhibition of native *Littorina saxatilis* (Olivi) by introduced *L. littorea* (L.). Journal of Experimental Marine Biology and Ecology 105: 187–196.

Zahvatkin, J. A., 2001. Course of General Entomology. Kolos, Moscow (in Russian).