

# Long-term studies of *Littorina obtusata* and *Littorina saxatilis* populations in the White Sea

Long-term  
Population dynamics  
Demography  
*Littorina*  
Trematoda

Long term  
Dynamique de population  
Démographie  
*Littorine*  
Trématode

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## ABSTRACT

The results of a 14-year survey of the populations of *L. saxatilis* and *L. obtusata* from one locality in the Kandalaksha Bay of the White Sea are presented. The periwinkles were found to be hosts of 10 castrating trematode species. *Microphallus piriformes* was the most abundant species with infection prevalence often exceeding 50%. Year-to-year variation of the infection prevalence was correlated in the two host species, probably reflecting fluctuations in the influx of trematode eggs to the shore. Long-term changes in population density are associated with the variation of the age structure of the winkles, suggesting a dependence of the population density on the success of the recruitment. Fluctuations in abundance and age composition were correlated in *L. saxatilis* sub-populations inhabiting macrophytes, gravel and stone surfaces, but were asynchronous with changes in abundance and age composition of *L. obtusata* population. No significant influence of variations in trematode infection upon the hosts' abundance or age structure was found in either species of the winkles. It is assumed that despite a strong negative influence of trematodes on reproduction of the host individual, there are no disastrous consequences for the population level; this, in turn, suggests the existence of some compensating mechanisms ensuring a stability of the host-parasite co-action.

## RÉSUMÉ

Caractéristiques à long terme de populations de gastéropodes intertidaux *Littorina obtusata* et *Littorina saxatilis* dans la mer Blanche.

Des populations de *L. saxatilis* et *L. obtusata* de la baie de Kandalaksha, dans la mer Blanche, ont fait l'objet d'une étude de 14 ans dont les résultats sont présentés. Les littorines sont les hôtes de dix espèces de trématodes qui provoquent leur castration: l'espèce la plus abondante, *Microphallus piriformis* a une fréquence de contamination qui dépasse souvent 50%. Les variations interannuelles de la contamination sont corrélées chez les deux espèces-hôtes, et suivent probablement les fluctuations de l'arrivée des œufs de trématodes sur la côte. Les variations à long terme dans la densité des populations sont associées aux variations de leurs structures en âges et suggèrent une corrélation entre la densité de population et le succès du recrutement. Les fluctuations dans

l'abondance et la structure en âge sont corrélées dans les sous-populations de *L. saxatilis* habitant des surfaces de macrophytes, gravier et roche, mais ces indices ne sont pas corrélés pour *L. obtusata*. Aucune des deux espèces de littorines ne présente d'effet significatif entre les variations de la contamination et l'abondance des hôtes ou la structure en âges. L'effet négatif important des trématodes sur la reproduction individuelle de l'hôte n'a probablement pas de conséquence désastreuse à l'échelle de la population, ce qui suggère l'existence de mécanismes compensateurs garantissant une stabilité dans la co-habitation entre l'hôte et le parasite.

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## INTRODUCTION

Investigation of the dynamic patterns of two (or more) genetically related and ecologically similar species living in the same environment has attracted the special attention of researchers since the middle of the present century (Clarke, 1960, 1962). This subject is of great interest, providing as it does an insight on the influence of the same environmental selective forces on similar, though not identical population systems. Classical examples of this kind of studies performed on coexisting populations of the land snails are found in the works on *Cepaea* spp. (Bantock *et al.*, 1975; Wallace, 1978; Arthur, 1978, 1980; Cowie and Jones, 1987; Mazon *et al.*, 1989) and *Partula* spp. (Johnson *et al.*, 1977). Populations of marine molluscs have received much less attention in this respect.

The intertidal prosobranchs *Littorina saxatilis* and *Littorina obtusata* are convenient model subjects for a study of the dynamic patterns in populations of closely related species. They form dense coexisting colonies on many shores of the North Atlantic and Arctic coasts (Matveeva, 1974), including the White Sea. An especial interest for the study of these species is provided by the fact that in the White Sea populations, *L. saxatilis* and *L. obtusata* have trematode parasites in common, often occurring with a high prevalence. Trematodes are assumed to be an important selective agent, since they have a powerful impact on host reproduction (through a parasitic castration) and survival (Hurd, 1990). It is often stressed in ecological studies that parasites are a heavy burden for the population to bear and that they may have a strong influence upon the host population dynamics. However, a quantitative estimation of the degree of this influence is rarely attempted in the natural populations.

Since 1982, we have carried out a long-term populational investigation of *L. obtusata* and *L. saxatilis* in the White Sea. The aim of the present paper is to disclose some of the main results obtained during a 14-year survey of the population structure and dynamics of *L. obtusata* and *L. saxatilis* populations in the White Sea. In this paper, we shall concentrate mainly on the structure and dynamic patterns in coexisting *L. obtusata* and *L. saxatilis* populations, attempting to estimate a degree of correspondence between the changes in the population parameters in these two species and to relate these changes to the variation in infection prevalence.

## MATERIALS AND METHODS

### Studied species

The prosobranchs *L. obtusata* and *L. saxatilis* are abundant species found in the intertidal zone of North Atlantic and Arctic shores (Matveeva, 1974; Raffaelli, 1982).

The periwinkles are dioecious. The longevity of *L. obtusata* in the White Sea is 8 to 11 years, and that of *L. saxatilis* – 7 to 9 years (Sergievsy *et al.*, 1991). *L. obtusata* becomes mature at 3-4 years; the age of maturation of *L. saxatilis* is 2-3 years (Granovitch and Sergievsy, 1990). Fertilization is internal. Both species of periwinkle are direct developers. *L. obtusata* lays benthic egg masses, and *L. saxatilis* is an ovoviviparous species (Matveeva, 1974). The mobility of adults is low (1-3 m) (Janson, 1983), so the progeny is very likely to remain in the "parental" local population.

In the White Sea, *L. saxatilis* and *L. obtusata* are intermediate hosts of 10 trematode species belonging to 5 families (Galaktionov and Dobrovolsky, 1984; Sergievsy, 1985): family Microphallidae-*Microphallus piriformes*, *M. pygmaeus*, *M. pseudopygmaeus*, *M. triangulatus*, *Microphallus* sp.; family Opecoelidae-*Podocotyle atomon*; family Echinostomatidae-*Himasthla* sp.; family Rencolidae-*Renicola* sp.; family Notocotylidae-*Notocotylus* sp.; family Heterophyidae-*Cryptocotyle lingua*.

### Study site

The study site is situated on a moderately sheltered stony beach of Ryazhkov Island in the North Archipelago region in the Kandalaksha Bay of the White Sea (67° 00' 12" N 32° 34' 36" E). The tidal range is 1.8-2.2 m. The intertidal zone is covered by boulders and stone, the spaces between them being filled with gravel and sand. Brown macroalgae occupy the lower part of the intertidal zone, forming a belt of 30-40 m width. *Ascophyllum nodosum* and *Fucus serratus* are present in the lower part of the fucoid belt, whereas *Fucus vesiculosus* dominates in the upper part. In the lower intertidal horizon, filamentous algae and blue mussel beds often occur. This vertical zonation was typical for this site throughout the study period, though the biomass of algae and mussels varied.

Relative areas of various substrates differed in different years. However, there were some general features in their mosaic distribution: in the horizon occupied by *A. nodosum* and in the lower part of the *F. vesiculosus* horizon, fucoids

covered 90 to 100% of the area, whereas in the upper part of the *F. vesiculosus* canopy, areas of the furoids altered with gravel and stone spots. Above the furoid belt, a zone of gravel and stones was situated.

### Sampling procedure

Sampling was performed annually in August-September of 1982-1995 (except 1990). Distribution of the main substrates (including shape and relative area occupied by the substrate) in the intertidal zone was mapped. Snails were collected quantitatively at low tide from three substrate types: 1) the furoid canopy; 2) from gravel; and 3) from stone surfaces. All samples were collected from a 1/40 m<sup>2</sup> area and placed in separate plastic bags. For the furoid belt, all seaweeds were cut off and taken together with the upper layer (2-3 cm in depth) of underlying sediment. For the second substrate, the upper layer (2-3 cm) of gravel was sampled. Snails from the stone surfaces were carefully hand-collected. The number of samples varied annually from 24 to 100.

In the laboratory, samples were sieved through the soil sieve with 1 mm mesh size. All periwinkles were sorted out of samples, shell diameter was measured and the age of each mollusc recognized by annual growth checks (which appear in spring when growth is resumed after the winter interruption) was determined. In the very few cases where age determination was difficult because of partial destruction of growth checks, these molluscs were assigned to age groups according to size. All snails greater than one year of age were dissected using a binocular microscope in order to determine sex and to identify the species of trematode parasites (if present). The total number of dissected snails ranged from 1 000 to 3 000 ind. in different years.

### Statistics

Non-parametric statistical procedures were used, because assumptions about the normal distribution and homoscedasticity were violated in most studied variables (Sokal and Rohlf, 1995).

## RESULTS

### Population density

The spatial variation of population density of the periwinkles revealed clear substrate heterogeneity. The microhabitat preferences of *L. saxatilis* and *L. obtusata* are different. In fact, *L. obtusata* was found only on the macroalgae, whereas *L. saxatilis* occupied gravel and stone surfaces, as well as the furoid canopy (Fig. 1).

The population density of the periwinkles varied considerably (Fig. 1). Between-years differences in the population density of *L. saxatilis* estimated by the Kruskal-Wallis test statistics (K-W) were highly significant for the samples from three kinds of substrata ( $p < 0.0001$  in all cases). In *L. obtusata*, between-years variability

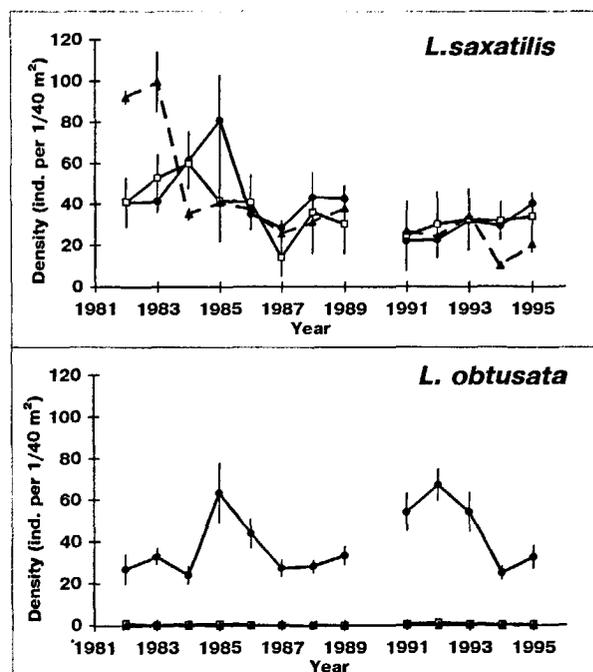


Figure 1

Long-term dynamics of the mean population density of the *L. saxatilis* and *L. obtusata* sub-populations localized on different substrates of Ryazhkov Island (White Sea). Circles – samples from the macrophytes, squares – from the gravel, and triangles – from the stone surfaces. Vertical bars represent standard error. No bar means that standard error is less than the symbol size.

of the population density was significant only for samples from the furoid canopy (K-W:  $p < 0.0001$ ). The abundance of *L. saxatilis* was positively correlated in different microhabitats. In this species, the Spearman's rank correlation ( $R_s$ ) between mean densities in the samples from macroalgae and gravel was 0.776 ( $p < 0.002$ ); between those on the furoids and the stone surfaces  $R_s = 0.635$  ( $p < 0.02$ ); and in the samples from gravel and stone surfaces  $R_s = 0.610$  ( $p < 0.03$ ). In contrast, no association was found between long-term variations of the abundances of *L. saxatilis* and *L. obtusata* on either substratum (Spearman's rank correlation:  $p > 0.10$ ).

### Age structure

The spatial distribution of snails of different ages was heterogeneous. In *L. obtusata* populations, the youngest snails (1-2 years old) mostly occurred in the upper part of the furoid belt, on *F. vesiculosus*, and were rare in the samples from *A. nodosum*. A small increase in number of the young *L. obtusata* was also found in the samples taken from the lowest intertidal horizon, where filamentous algae were present. In the *L. saxatilis* population, great variability of age structure was found for different substrates. The youngest snails were localized mainly on the gravel, whereas older snails preferred the furoid canopy as habitat (Granovitch *et al.*, 1987; Sergievsky, Granovitch, 1989; Sergievsky *et al.*, 1991). The age composition of samples from the stone surfaces varied and was dependent on the presence of potential shelters: crevices, empty barnacle shells etc. (Granovitch and Sergievsky, 1989).

In the *L. saxatilis* population, the mean age of snails (adopted as an integral measure of the age composition) was generally the lowest in the samples from gravel, in accordance with the predominant localization of the juveniles in this microhabitat (Fig. 2). It was found that long-term changes of the mean age of the individual were significantly correlated in *L. saxatilis* sub-populations from different substrata:  $R_s = 0.868$ ,  $p < 0.0002$ , between the samples from fucoids and gravel;  $R_s = 0.648$ ,  $p < 0.02$ , for the fucoids and the stone surfaces; and  $R_s = 0.835$ ,  $p < 0.001$ , for the gravel and stone surfaces. The mean age of *L. saxatilis* was not correlated with that of *L. obtusata* over the study period ( $R_s = 0.429$ ,  $p > 0.14$ , for the samples from the fucoid canopy), thus suggesting that changes of the age composition of these two species were not synchronized.

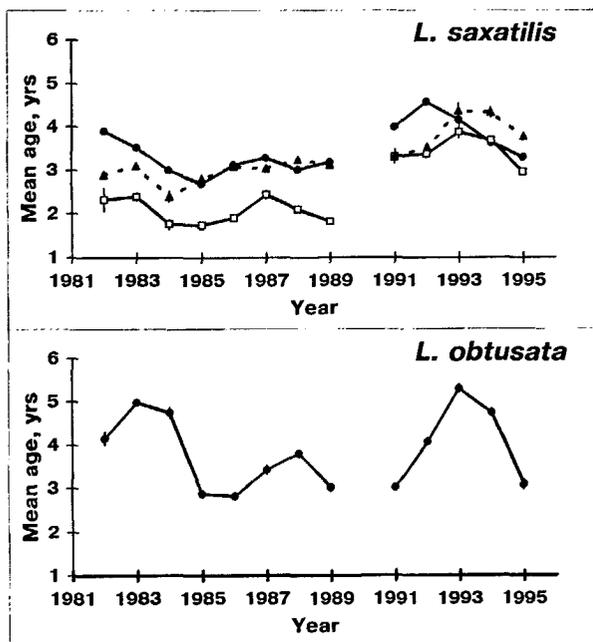


Figure 2

Long-term variations of the mean age of the sub-populations of the periwinkles localized on different substrates of Ryazhkov Island (White Sea). Circles – samples from the macrophytes, squares – from the gravel, and triangles – from the stone surfaces. Vertical bars represent standard error. No bar means that standard error is less than the symbol size.

In *L. saxatilis* populations, the negative correlation between the population density and the mean age of snails was found ( $R_s$  was  $-0.775$ ,  $-0.589$ ,  $-0.626$  for the samples from the fucoid canopy, the gravel, and the stone surfaces, respectively,  $p < 0.04$ ). Thus, over the study period, the population density of *L. saxatilis* was higher, when the juveniles were abundant. This suggests that population density dynamics is mainly determined by the success of recruitment. Similarly, in *L. obtusata* the Spearman's rank correlation between the mean age of the individual and the population density on the fucoids was  $-0.341$ , though this was not statistically significant ( $p > 0.25$ ).

## Sex ratio

The sex ratio in populations of *L. obtusata* and *L. saxatilis* is biased towards females. In both species, the proportion of females increases with age, so that females largely dominate among old snails (Granovitch and Gorbushin, 1995). No spatial heterogeneity of the sex ratio was found in the studied populations. In some years, the proportion of females in the winkle populations may increase up to 60–65% (Fig. 3). Long-term changes in the relative abundance of males were not correlated in the two species ( $R_s = 0.441$ ;  $p > 0.13$ ). No significant correspondence (as estimated by the Spearman's rank correlation) was found between the changes of sex ratio and the long-term dynamics of the population density, or that of the age composition.

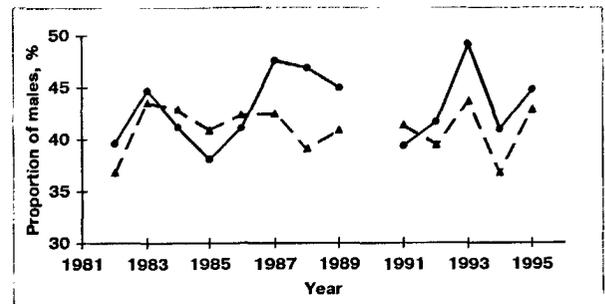


Figure 3

Long-term variation of the sex ratio in populations of *L. saxatilis* and *L. obtusata* from Ryazhkov Island (White Sea). Samples from the fucoids. Circles and solid line – *L. saxatilis*, triangles and broken line – *L. obtusata*.

## Trematode infection prevalence

High levels of trematode infection were observed in the studied populations of *L. obtusata* and *L. saxatilis*. Trematode species composition and relative weight of each species in the total infection prevalence of the host population were similar for *L. saxatilis* and *L. obtusata* (Sergievsy, 1985; Granovitch, 1992). Microphallids of the "pygmaeus" species complex (*Microphallus piriformes*, *M. pygmaeus*, *M. pseudopygmaeus* and *M. triangulatus*, of which *M. piriformes* is the commonest) account for the high infection levels in the populations of periwinkles. Infection by the "pygmaeus" species complex reached 50% and more. Metacercariae of these closely related species develop in daughter sporocysts. The infection of the definitive host (common eider and some other species of intertidal feeding birds) occurs without involvement of a second intermediate host (Galaktionov and Dobrovolsky 1984; Galaktionov, 1993). Other trematode species have free-living cercariae in the life cycle. Infection prevalence of these species was usually about 3–5%.

There was a tendency for the infection prevalence by microphallids of the "pygmaeus" group to increase in the middle and upper part of the fucoid belt, but this pattern showed some year-to-year variability (Mikhailova *et al.*, 1988). However, for *L. saxatilis*, consistent differences in infection by *M. piriformes* were found between the stone

surfaces and other substrates. Infection by *M. piriformes* of snails collected from stone surfaces was the highest (up to 80-100%). Differences in trematode infection between samples from the gravel and the furoid canopy were found when different age groups of snails were considered. Young snails had lower infection prevalences on the gravel, whereas trematode infection of old snails was lower for samples from the furoids (Sergievsky *et al.*, 1984; Mikhailova *et al.*, 1988; Granovitch, 1992).

Trematode infection varied between different age groups of *L. saxatilis* and *L. obtusata*. The lowest infection levels were typical for young snails (2-3 years), and infection prevalence increased with age. In some years, the prevalence of microphallids of "pygmaeus" species complex was found to decline in the oldest snails, so that the heaviest infection was observed in the middle-aged (5-6 years) molluscs. It is worth noting that no age-specific differences in infection levels were found for the immature, non-invasive stages of the microphallids. Infection by the species with free-living cercariae consistently revealed an increase with the host age in the studied populations (Granovitch *et al.*, 1987).

Sex-specific differences in trematode infection, although not always significant, were found in the populations of periwinkles (Granovitch and Gorbushin, 1995). In general, infection of females is higher than in males. Sex-specific differences in infection prevalence were dependent on the host age: more females than males were infected in the young age groups; and the converse was observed in the old snails. This pattern was rather consistent, although not always as significant (Granovitch and Gorbushin, 1995).

The trematode infection of *L. obtusata* and *L. saxatilis* showed considerable long-term variations (Fig. 4). Infection prevalence was correlated neither with the population density of the littorines of the same, nor with that of the following year (Spearman's rank correlation:  $p < 0.05$ ). Despite large year-to-year fluctuations, infection levels never declined below 40% in either species of winkle; this suggests high parasitic pressure on the host populations throughout the study period. A positive association between long-term changes in infection prevalence was found in the two host species when either the prevalence of *M. piriformes*, or the infection by the immature microphallids of "pygmaeus" group was considered ( $R_s = 0.835$ ,  $p < 0.0004$  and  $R_s = 0.643$ ,  $p < 0.02$ , respectively). No significant relation was detected between the prevalence of *M. piriformes* and the level of the immature microphallid infection in the same, or in the previous year (Spearman's rank correlation:  $p < 0.20$ ).

As infection by the castrating trematodes has a direct impact on host reproduction (Hurd, 1990), it might be expected that years of severe infection in the winkle populations would be followed by years of poor recruitment. In order to test this hypothesis, the infection level of the year  $N$  was related to the mean age of the snails in the year  $N+1$ . This correlation did not significantly differ from zero in the *L. saxatilis* sub-population from the furoid canopy ( $R_s = -0.073$ ,  $p > 0.80$ ). Surprisingly, in the *L. obtusata* population a negative correlation was found between the infection level and the mean age of the

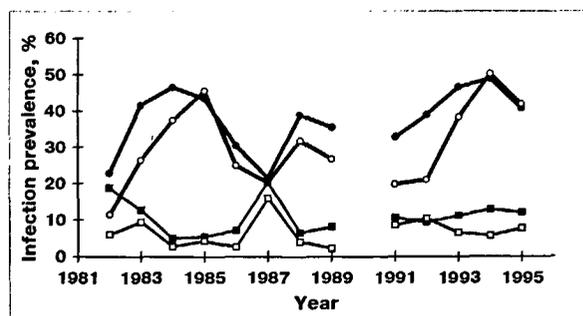


Figure 4

Long-term dynamics of trematode infection prevalence in the populations of *L. saxatilis* and *L. obtusata* from Ryazhkov Island (White Sea).

Samples from the macrophytes. Circles – infection by invasive *Microphallus piriformes*, squares – infection by undeveloped (immature) parthenites of the microphallids of "pygmaeus" group. Filled symbols represent *L. saxatilis*, open symbols – *L. obtusata*.

population in the following year ( $R_s = -0.618$ ,  $p < 0.05$ ). This means that the situation is contrary to the expected one: years of heavy infection tend to be followed by years with a high abundance of juveniles and thus, a low mean age of the individual.

## DISCUSSION

Vertical zonation and substrate heterogeneity are probably the most important features in the spatial distribution of the periwinkles in the intertidal zone of the White Sea. Spatial distribution and microhabitat preferences are probably determined by behavioural mechanisms such as active habitat choice. We suggest that observed differences in the age structure of *L. saxatilis* in samples collected from various substrates may reflect the relative availability of shelters to snails of different sizes: small snails can hide themselves in small spaces between gravel and sand particles, whereas larger periwinkles can find shelter only in the substrate with larger "pores" such as the furoid canopy (Mikhailova *et al.*, 1988). A similar habitat-choice mechanism is probably responsible for the occupying of empty barnacle (*Semibalanus balanoides*) shells by snails of size corresponding to the size of entrance into the shell (Granovitch and Sergievsky, 1989).

An important aspect of the influence of trematodes on the snail host is a parasite-induced modification of the behaviour of periwinkles infected by *M. piriformes*. Our experiments suggest that trematode infection suppresses tidal migration of the snails and results in the predominant localization of infected snails in the open microhabitats (mostly the stone and macrophyte surfaces) at low tide (Sergievsky *et al.*, 1984; Mikhailova *et al.*, 1988). These changes in behaviour probably increase the chances of infected periwinkles being eaten by the definitive host of *M. piriformes*.

In general, we suppose that active habitat choice and parasite-induced modification of host behaviour may be two independent mechanisms that are responsible for the heterogeneous spatial distribution of the winkles. At low tide, large uninfected *L. saxatilis* probably move into the thickness of the furoid canopy, and small uninfected snails into "pores" in gravel (Mikhailova *et al.*, 1988). Some small uninfected snails may hide themselves in the empty barnacle shells on stone surfaces (Granovitch and Sergievsky, 1989). Plain stone surfaces exposed to avian predators are mostly occupied by *L. saxatilis* carrying the mature metacercariae of *M. piriformes* (Sergievsky, Granovitch, 1989; Sergievsky, 1992).

An important feature of the intertidal zone of the White Sea is the prolonged (up to 7-month) ice cover. Low temperatures and ice shifts due to tidal movements impair the activity of the intertidal snails and make it impossible to maintain the spatial distribution typical for summer months. Our observations and data from literature (Matveeva, 1974) indicate that the microhabitat distribution of *L. saxatilis* and *L. obtusata* described above establishes itself annually in spring when the periwinkles recover from winter inactivity.

Matched changes in the abundance and the age structure of the littorines populations suggest a fluctuating nature of repopulation, with alternating periods of successful and poor recruitment. It is worth noting that correspondence in the long-term dynamics of the abundance and age composition between the sub-populations of *L. saxatilis* localized on different substrata suggests that these sub-groups respond to environmental cues as the parts of an integrated population entity. In contrast, this association was lacking when changes either of population density or of age composition were compared between populations of *L. saxatilis* and *L. obtusata*. As the dynamics of major ecological factors within the studied part of the littoral (only few metres wide) is similar, this may suggest some intrinsic mechanisms (e.g. the differences in ecological requirements or tolerance) that govern the asynchronous changes in the population structure of these closely related species.

Infection prevalence showed great variation during the 14-year study, and these variations coincide in populations of both host species. This is probably a reflection of changes in the infection influx to the snail populations related to the population density and infection levels of the final hosts. Indeed, the long-term study of the populations of the definitive host of most trematodes found in the periwinkles (common eider *Somateria mollissima* and some other shore-feeding birds) in the North Archipelago region showed great year-to-year variability of population density and trematode infection prevalence (Karpovich, 1979).

Trematode infection is an important factor impairing the reproductive ability of the intermediate hosts (Hurd, 1990) and effecting survival of the snails under stressful environmental conditions (Sergievsky *et al.*, 1986; Galaktionov, 1993). Microphallids of the "pygmaeus" species complex cause an irreversible castration of the infected periwinkles and thus withdraw a large part of the population (up to 50% in the studied locality) from reproduction. Moreover, infected snails can survive at least for a year (Granovitch and Sergievsky, 1990) and may compete with uninfected individuals for food and other life resources. Hence, these trematodes are potentially a very important factor influencing the populations of *L. obtusata* and *L. saxatilis*. Surprisingly, no negative influence of the trematode infection on the abundance or the recruitment success of the studied hosts' populations was detected. This suggests the existence of certain compensating mechanisms that support the persistence of these populations under conditions of severe parasitic pressure. Immigration from some source population is not a likely explanation for this, because the areas adjacent to the studied locality also have a high infection level (pers. obs.), as a natural consequence of the high mobility of the definitive hosts (*Somateria mollissima*), contaminating with trematode eggs large areas of the shore. We suggest that the main source term in the population dynamics of the winkles is a recruitment of the juveniles produced "on the spot". A possible mechanism (but surely not the only one) compensating for the substantial reduction in the abundance of potentially fertile individuals due to trematode castration may be an increase in the reproductive output of the remaining fertile part of the population. Some evidence of this is available from the study of *L. saxatilis* populations where the number of embryos in the brood pouch of females was found to be higher in the heavily infected population as compared to those with low and intermediate infection levels (Sokolova, 1995).

In summary, the results presented suggest the stability of host-parasite co-action in communities. A strong negative influence of trematodes on reproduction of the host individual has no disastrous consequences for the population level, and the studied host-parasite system exists for at least 14 years.

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## REFERENCES

- Arthur W. (1980). Further associations between morph-frequency and coexistence in *Cepaea*, *Heredity* **22**, 117-139.
- Arthur W. (1978). Morph-frequency and coexistence of *Cepaea*, *Heredity* **11**, 335-346.
- Bantock C.R., J.A. Bayley, P.H. Harvey (1975). Simultaneous selective predation on two features of a mixed sibling species population, *Evolution* **29**, 636-649.
- Clarke B.C. (1960). Divergent effects on natural selection on two closely related polymorphic snails, *Heredity* **14**, 423-443.
- Clarke B.C. (1962). Natural selection in a mixed populations of two polymorphic snails, *Heredity* **17**, 319-345.
- Cowie R.H., J.S. Jones (1987). Ecological interactions between *Cepaea nemoralis* and *Cepaea hortensis*: competition, invasion but no niche displacement, *Functional Ecology* **1**, 91-97.
- Galaktionov K.V. (1993). Life cycles of trematodes as the components of communities (an experience of analysis with members of family Microphallidae as example), Russian Academy of Sciences Publishing Co., Apatity, 190 p. [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: Ecologo-parasitological investigations of the northern seas (*Ekologo-parazitologicheskiye issledovaniya severnykh morey*), ed. by Yu. I. Polansky, Apatity, 8-41. [In Russian].
- Granovitch A.I. (1992). The effect of trematode infection on the population structure of *Littorina saxatilis* (Olivi) in White Sea, in: Proceedings of the Third International Symposium on Littorinid Biology, ed. by J. Grahame, P.J. Mill, D.G. Reid, Malacological Society of London, London, 255-263.
- Granovitch A.I., A.M. Gorbushin (1995). Differences in trematode infection between males and females of intertidal gastropods of genera *Hydrobia* and *Littorina*, *Parazitologiya* **29**, 167-178. [In Russian].
- Granovitch A.I., N.A. Mikhailova, S.O. Sergievsky (1987). Age-specific peculiarities of infection in populations of intertidal molluscs *Littorina obtusata* and *Littorina saxatilis* by the trematode parthenites, *Parazitologiya* **21**, 721-729. [In Russian].
- Granovitch A.I., S.O. Sergievsky (1989). The use of barnacle settlements as a shelter for snails *Littorina saxatilis* (Gastropoda, Prosobranchia) in relation to the trematode infection, *Zoologicheskij Zhurnal* **68**, 39-47. [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].
- Hurd H. (1990). Physiological and behavioural interactions between parasites and invertebrate hosts, *Advances in parasitology* **29**, 271-318.
- Janson K. (1983). Selection and migration in two distinct phenotypes of *Littorina saxatilis* in Sweden, *Oecologia* **59**, 58-61.
- Johnson M.S., B.C. Clarke, J. Murray (1977). Genetic variation and reproductive isolation in *Partula*, *Evolution* **31**, 116-126.
- Karpovich V.N. (1979). Changes in abundance of the common eider in Kandalaksha Nature Reserve and its possible relations with the overall dynamics of the eider populations in north and north-west of the Europe, in: Ecology and morphology of common eider in the USSR (*Ekologiya i morfologiya gag v SSSR*), Moscow, Nauka, 38-45. [In Russian].
- Matveeva T.A. (1974). Ecology and life cycles of common gastropod species in the Barenz and the White Seas, in: Seasonal phenomena in the life of the White and the Barents Seas. Investigations of the fauna of seas (*Issledovaniya fauny morey. Sezonnyye yavleniya v zhyzni Belogo i Barentseva morey*), ed. by B.E. Bykhovskiy, Nauka, Leningrad, **13**, 21, 65-190. [In Russian].
- Mazon L.L., M.A.M. de Pancorbo, A. Vicario, A.I. Aguirre, C.M. Lostao (1989). Selection in sympatric population of *Cepaea*, *Genet Sel Evol.* **21**, 269-281.
- Mikhailova N.A., A.I. Granovitch, S.O. Sergievsky (1988). The influence of trematode invasion on the microhabitat distribution of molluscs *Littorina obtusata* and *L. saxatilis*, *Parazitologia* **22**, 398-407. [In Russian].
- Raffaelli D. (1982). Recent ecological research on some european species of *Littorina*, *J. Moll. Stud.* **48**, 342-354.
- Sergievsky S.O. (1985). Populational approach to the analysis of the periwinkle *Littorina obtusata* (L.) invasion with trematode parthenites, *Helminthologia* **22**, 5-14.
- Sergievsky S.O., A.I. Granovitch (1989). Spatial heterogeneity in the population structure of intertidal mollusk *Littorina saxatilis* (Olivi), *Proceedings of Zoological Institute of Academy of Sciences of USSR (Trudy Zoologicheskogo Instituta AN SSSR)*, **203**, 146-168. [In Russian].
- Sergievsky S.O., A.I. Granovitch, N.A. Mikhailova (1984). Heterogeneous distribution in the littoral zone of the molluscs *Littorina obtusata* and *L. saxatilis* (Gastropoda: Prosobranchia) infected by trematode parthenites, *Zoologicheskij Zhurnal* **63**, 929-931.
- Sergievsky S.O., A.I. Granovitch, N.A. Mikhailova (1986). Influence of trematode infection on the survival of molluscs *Littorina obtusata* and *L. saxatilis* under conditions of extremely lowered salinity, *Parazitologiya* **20**, 202-207. [In Russian].
- Sergievsky S.O., A.I. Granovitch, N.A. Mikhailova (1991). Age structure of the populations of intertidal snails *Littorina saxatilis* and *L. obtusata* in the White Sea, *Proceedings of Zoological Institute of Academy of Sciences of U.S.S.R. (Trudy Zoologicheskogo Instituta AN SSSR)*, **233**, 79-126. [In Russian].
- Sokolova I.M. (1995). Influence of trematodes on the demography of *Littorina saxatilis* (Gastropoda: Prosobranchia: Littorinidae) in the White Sea. *Diseases of Aquatic Organisms* **21**, 91-101.
- Wallace A. (1978). Morph-frequency and co-existence in *Cepaea*, *Heredity* **41**, 335-346.