

The effect of trematode parthenitae on the growth of *Onoba aculeus*, *Littorina saxatilis* and *L. obtusata* (Gastropoda: Prosobranchia)

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To determine whether modern theories predict snail growth responses to trematode infestation a field growth study of *Onoba aculeus*, *Littorina saxatilis* and *L. obtusata* infected with two closely related Microphallidae trematodes was conducted in the White Sea. In each of the three host–parasite combinations studied trematode infection causes inhibition of snail reproduction. However, contrary to the classical interpretation of the gigantic growth of infected snails as a side effect of parasitic castration, the presented study failed to demonstrate that *Microphallus piriformes* causes gigantism in *Littorina*. The infection tended to stunt growth in *L. obtusata* and had no significant effect on growth rate of *L. saxatilis*. In contrast, gigantic growth was observed in *O. aculeus* infected with *M. pseudopygmaeus*. Considering that both trematode species are very similar biologically, the discrepancy is attributed to differences in the life history of the snail's hosts. *Onoba aculeus* is a relatively short-lived snail (2.5–3 y). The lifespan of *L. saxatilis* and *L. obtusata* is much longer (up to 9–11 y). These findings agree with a previously reported 'energetic' hypothesis that predicts growth alterations in accordance with life history variations of the snail species.

INTRODUCTION

Trematode parthenogenetic generations (sporocysts and rediae) infecting snails have been shown to cause changes in host growth rate (Sousa, 1983; Minchella, 1985; Gorbushin, 1997). Several studies have provided evidence of stunting effect of trematode infections (Moose, 1963; Sturrock & Sturrock, 1970; Sousa, 1983; Fernandez & Esch, 1991) whereas others have shown increased growth rates among infected specimens (Rothschild & Rothschild, 1939; McClelland & Bourns, 1969; Meuleman, 1972; Sluiters et al., 1980; Wilson & Denison, 1980; Mouritsen & Jensen, 1994; Huxham et al., 1995; Gorbushin, 1997). The phenomenon is usually connected with inhibition of snail reproduction (castration) (Sousa, 1983; Minchella, 1985) and it has been demonstrated that the growth rate correlates with the level of parasitic castration of a snail host (Gorbushin, 1997).

The existing hypotheses—'adaptive' (Minchella, 1985) and 'nonadaptive' (Sousa, 1983)—attempting to explain the alterations in host growth operate with life history variations of snail species and predict different growth responses to infestation in semelparous and iteroparous molluscs. Most of the observations forming the basis of those views involved comparisons of the growth of healthy snails with ones infected with single species of parthenitae. Few researchers have adopted the approach of Sousa (1983)—comparing a growth response of certain snail hosts following infestation with different trematode species. However, this approach looks quite productive. For example, it has been demonstrated that the growth response of infected *Hydrobia ulvae* varies significantly with the trematode species. Most probably due to its

lower pathogenicity, sporocystoid parthenitae induce increased host growth in contrast to redioid ones which cause no effect on growth rate (Gorbushin, 1997). This phenomenon produces the serious objection to both 'adaptive' and 'nonadaptive' hypotheses. In short, the differences between growth responses of infected semelparous and iteroparous snails may not be the result of different life histories but different pathogenicity of parthenitae parasitizing these groups of hosts.

One way of attacking this problem are comparative studies of growth responses of short-lived and long-lived snail hosts following the infestation with the same or biologically similar trematode species. The growth study of *Littorina saxatilis* (Olivi, 1792) (Prosobranchia: Littorinidae), *L. obtusata* (Linnaeus, 1758) (Prosobranchia: Littorinidae), *Onoba aculeus* Gould, 1841 (Prosobranchia: Onobidae) infected with trematodes of 'pygmaeus' group (Microphallidae) was undertaken to use this approach therefore testing the principal idea of both concepts—significant role of host life history variations in affecting the phenomenon of growth alteration in infected snails.

MATERIALS AND METHODS

Study systems

The investigation was carried out in the Chupa Inlet, Kandalaksha Bay of the White Sea (Russia) in late August 1996. All three prosobranch species studied are dioecious and direct developers; show habitat selection with regard to the type of substrate but coexist at some extension of intertidal zone.

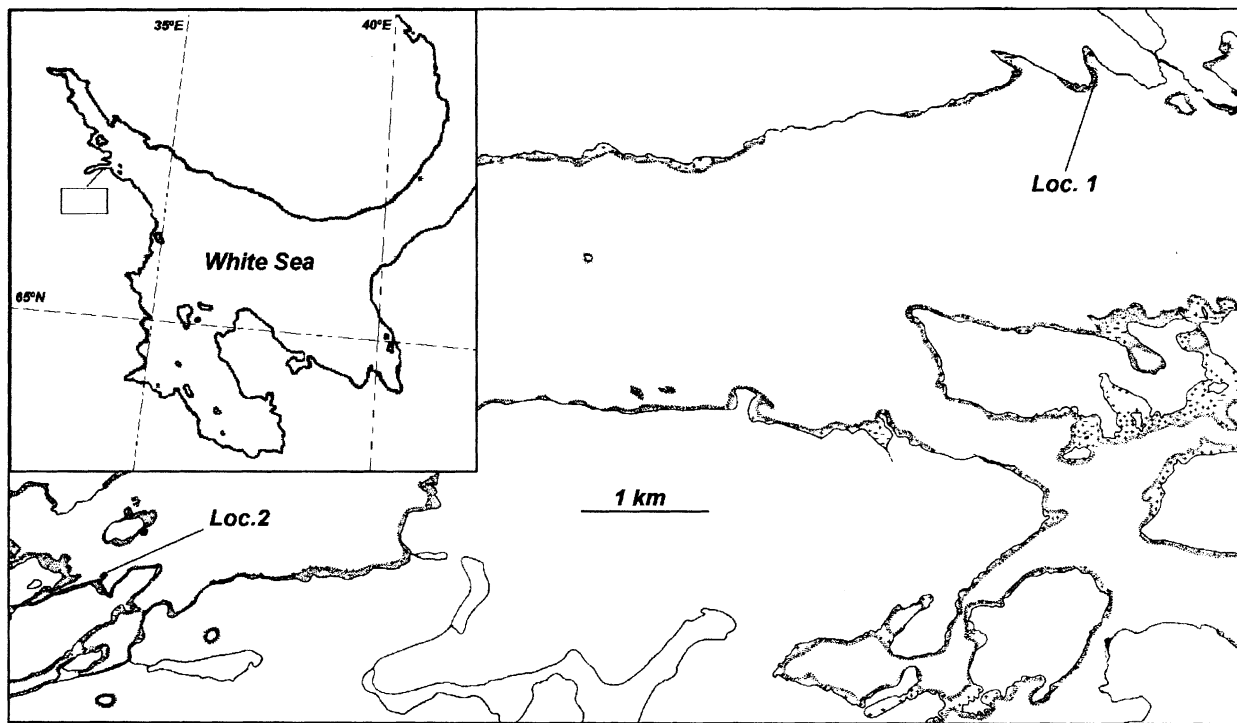


Figure 1. Map of sampling locations (see text).

Onoba aculeus. Small-sized species, height up to 5 mm. It inhabits the low level of the intertidal zone and is common on muddy gravel covered by fucoids. The species is involved in *Fucus vesiculosus* + *Ascophillum nodosum* biocenosis and reaches a population density of up to 6570 ind m⁻². An oviparous species. Recruits come from July to September (Scarlato, 1987). The longevity is 2.5–3 y (unpublished data). In the studied area *O. aculeus* is the intermediate host of two trematode species—*Microphallus pseudopygmaeus* (Microphallidae) and *Notocotylus* sp. (Notocotylidae) (unpublished data).

Littorina obtusata. Is a middle-sized snail, shell height up to 12 mm. An oviparous species. Recruits appear in August–September (Scarlato, 1987). The longevity in the White Sea is 8–11 y (Sergievsky et al., 1991).

Littorina saxatilis. Shell height up to 12 mm. An ovoviviparous species. Recruits appear in August–September (Scarlato, 1987). The longevity in the White Sea is 7–9 y (Sergievsky et al., 1991).

The principal characteristics of ecology, population structure and trematode fauna of both periwinkle species in the White Sea is described by Granovitch (1992) and Sergievsky et al. (1997). All three snail species have no seasonal migrations and overwinter in anabiosis, forming aggregations beneath stones and sea grass.

Two closely related trematode species—*Microphallus piriformes* (Odner, 1905) (Galaktionov, 1983) and *M. pseudopygmaeus* (Galaktionov, 1980) belong to the most specialized genus of the evolutionary advanced Microphallidae family (Galaktionov & Dobrovolsky, 1987). They are very similar morphologically and ecologically. Due to minor morphological differences both were identified as *Microphallus pygmaeus* (Levinsen, 1881) by the

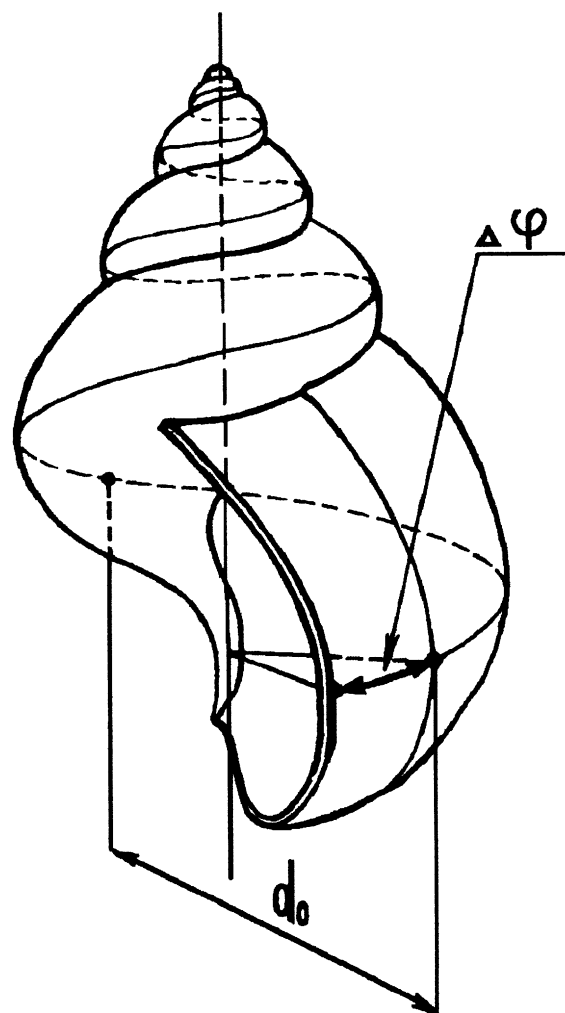


Figure 2. The diagram of a snail shell measurements (see text).

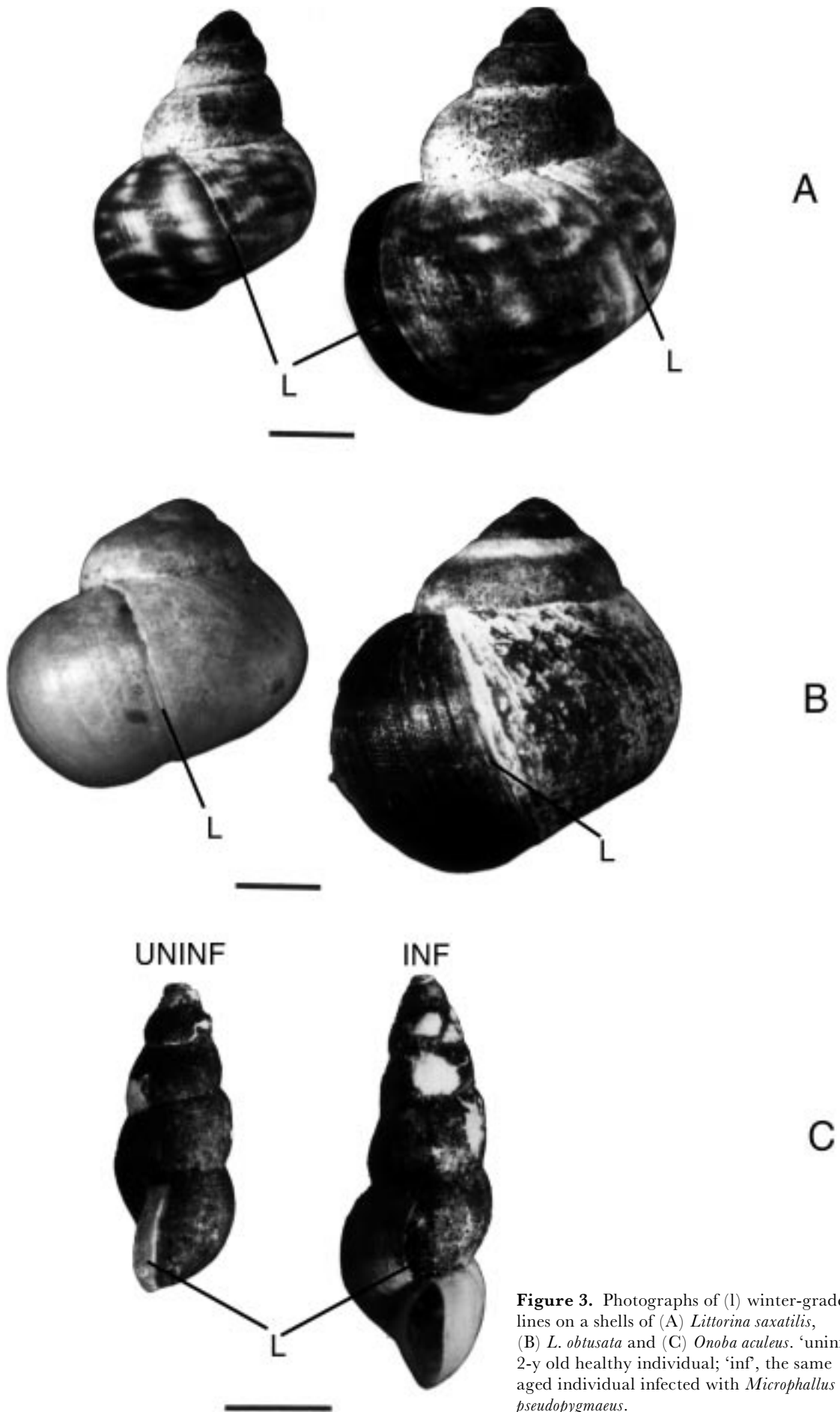


Figure 3. Photographs of (l) winter-grade lines on a shells of (A) *Littorina saxatilis*, (B) *L. obtusata* and (C) *Onoba aculeus*. 'uninf', 2-y old healthy individual; 'inf', the same aged individual infected with *Microphallus pseudopygmaeus*.

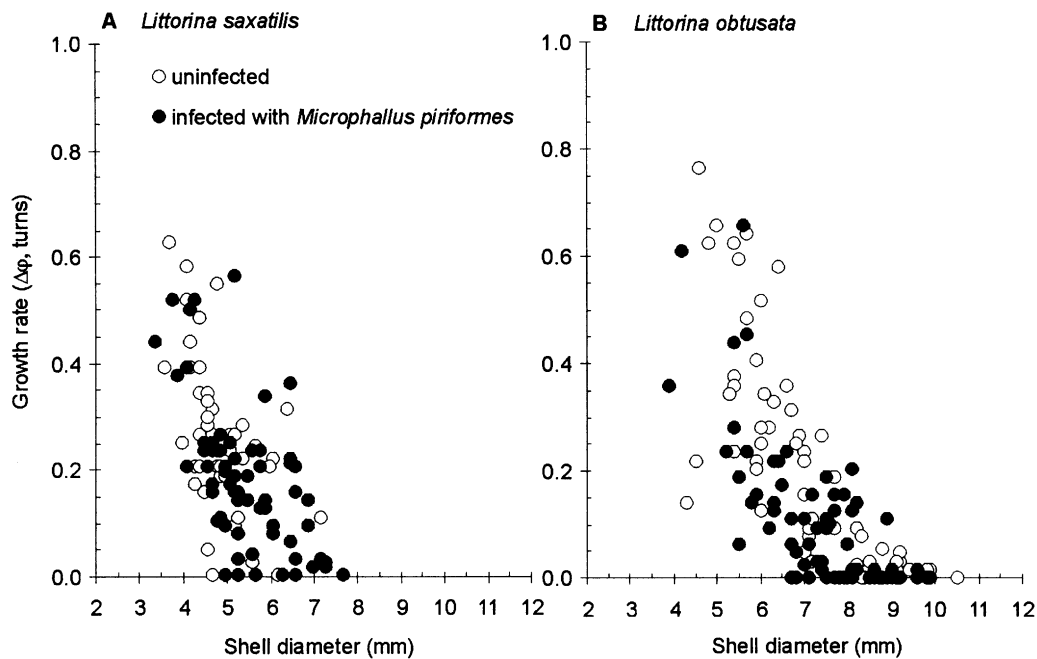


Figure 4. Growth rate ($\Delta\varphi$) of *Littorina saxatilis* (A) and *L. obtusata* (B) as a function of shell diameter (d_0).

early 1980s (Galaktionov, 1980, 1983, 1984). These species have identical life cycles: parthenogenetic generations (sporocysts) develop in marine intertidal gastropods; there is no second intermediate host and metacercariae mature inside daughter sporocysts; the definitive host—sea birds (usually *Somateria mollissima*)—can only become infected by eating an infected snail with mature metacercariae; molluscs are infected by swallowing trematode eggs. The development of the parasites inside the snail up to invasion stage occupies 1.5–2.0 months (Galaktionov, 1980, 1983, 1984).

Collection of animals

Littorina saxatilis and *L. obtusata* were sampled in Kruglaya Bay (Figure 1, loc. 1). The korga nearby Levin Navolok (a korga is the local name for the kind of bank exposed during low tide; Figure 1, loc. 2) was used for sampling of *O. aculeus*. Molluscs were sampled qualitatively in the middle horizon of the fucoid belt during low tide. One hundred and twenty-six *L. saxatilis* were collected by hand from upper and lateral surfaces of several stones, 133 *L. obtusata* were washed off from seaweed cut from the stones. Seventy-five *Onoba aculeus* were obtained by sieving removed sediment (muddy sand) lying between stones through sieves retaining snails larger than 0.5 mm. The sampled specimens were size-biased since mainly the larger individuals were collected in order to maximize the probability of finding infected ones.

Measurements and dissection

As a natural mark of beginning (late May) of snail growth season a last winter growth interruption line on a snail shell was used. The mechanism of formation on shells of the White Sea intertidal snails is described by Gorbushin, 1993. The following measurements were taken

from the snails' shell (Figure 2): shell diameter at the level of the last winter growth interruption line (d_0) (Figure 3A–C) and shell angle gain ($\Delta\varphi$) from the last winter interruption line to the rim of the shell aperture. Because the specimens were collected almost at the end of snail growth season (autumn frosts are possible from early September), angle gain from an identified last winter-grade line on the shell should be considered as an annual growth. All measurements were taken under the stereomicroscope using a standard ocular provided with a micrometer and an ocular angle meter. For angle growth measurement, the shell was vertically orientated so that the collumellar axis was perpendicular to the plane of measurements. The error of the diameter measurement did not exceed 0.05 mm and the angle gain was measured in *Littorina* sp. and *O. aculeus* with $\pi/32$ and $\pi/12$ accuracy respectively.

Following measurements, the shells were crushed and the specimens were sexed according to the presence or absence of penis. Also the size of the penis was estimated by measuring the length from base to the tip under the stereomicroscope. The abdominal soft parts of the specimens were subsequently dissected and examined for trematode infection. Trematode species were identified according to Galaktionov (1980, 1983, 1984). During examination the sexual maturity of the individuals was also determined. Each snail was examined for the presence of sexual products in the gonads (eggs in female and active spermatozooids in males).

Two-tailed *t*-test was used for comparison between mean penis sizes of infected and uninfected *L. saxatilis* and *L. obtusata* males. The proportion of males in *O. aculeus* population studied was low so the statistical analysis for this species was not performed.

Since growth rate decreases with snail size (see results), comparison of growth rates between infected and uninfected specimens was carried out by applying a paired

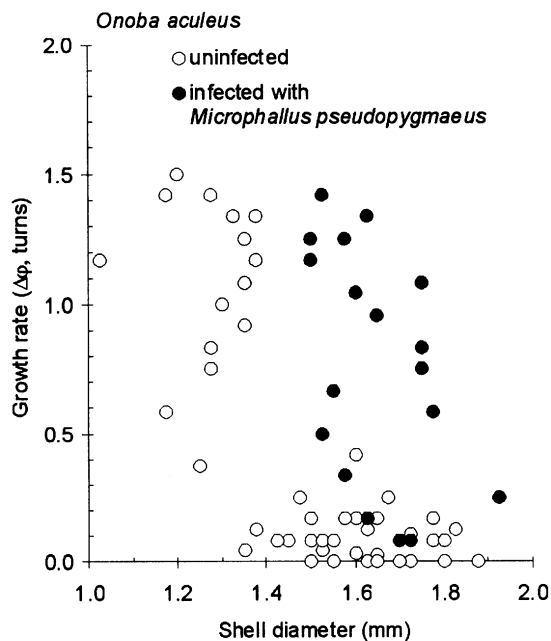


Figure 5. Growth rate ($\Delta\phi$) of *Onoba aculeus* as a function of shell diameter (d_0).

two-tailed *t*-test on pairs of snails with similar shell diameter at the last winter line (d_0). Pairs of snails were chosen randomly from the data base using computer algorithm. Due to possible growth rate differences between sexes only individuals with similar sex were paired. In case of *O. aculeus* only females were taken into the analysis.

RESULTS

The daughter sporocysts of *Microphallus pseudopygmaeus* were located in the *Onoba aculeus* gonads. *Microphallus piriformes* sporocysts were located in the gonad–digestive gland complex of both *Littorina* species. This type of localization leads to parasitic castration in both sexes. Microscopy of the gonads showed the absence of active spermatozooids in infected males in contrast to uninfected ones. Furthermore, infected males of both *Littorina* spp. exhibited significantly reduced penis size ($t_{22}=3.56$; $P<0.05$ —*Littorina saxatilis* and $t_{38}=8.26$; $P<0.0001$ —*L. obtusata*). The number of eggs and embryos in the reproductive systems of infected females of all three snail species varied from none to very few and was always less than in gonads of uninfected individuals.

The growth patterns of *L. saxatilis*, *L. obtusata* and *O. aculeus* are shown in Figures 4A,B & 5. The snails' growth rate correlates negatively with the individual shell size at the beginning of the growth season. The smaller shell diameter at the moment of winter-grade line formation, the higher angle gain at the date of sampling.

Infestation with *M. piriformes* had not induced any significant changes ($t_{65}=0.76$; $P>0.05$) in growth rate of *L. saxatilis* (Figure 4A). Growth rate of *L. obtusata* infected with the same species significantly ($t_{89}=2.49$; $P<0.02$) decreased in comparison with uninfected ones (Figure 4B). In contrast, *O. aculeus* infected with *M. pseudopygmaeus* displayed a significantly ($t_{18}=6.5$; $P<0.0001$) increased growth rate (Figure 5).

DISCUSSION

The very special mechanism of parthenogenetic generations development is typical for the 'pygmaeus' microphallides. The specific feature is very early parasitic castration of the host due to sprouting of sporocyst stolons directly to the snail gonad (Galaktionov, 1987). Daughter sporocysts of the 'pygmaeus' group are motionless and obtain all their nutrition from direct absorption through its tegumental surface. Thus, severe pathogenic pressure on the host during migration of sporocysts, cercariae and, moreover, rediae directly ingesting the host tissues is not characteristic of 'pygmaeus' parthenitae. These species are relatively low-pathogenic trematodes. Indeed, the infection with microphallides from the 'pygmaeus' group has no significant impact on the resistance of *Littorina saxatilis* to unfavourable environmental factors (Galaktionov, 1990). It was shown that infected and uninfected snails do not differ in resistance to heat stress and desiccation. Moreover, infected individuals are more resistant to subzero temperatures. Increased mortality of infected *Littorina* was only shown in some experiments on the resistance to low salinity. It is important to note that Galaktionov (1990) postulated low pathogenicity of 'pygmaeus' microphallides for *L. saxatilis* but not for *L. obtusata*. He proposed that these parasites have a significant role in selective mortality of snail species in the field.

In this study relatively higher pathogenicity of *Microphallus piriformes* for *L. obtusata* is supported by the fact of lowered host growth in this host–parasite combination. It is interesting to note that one and the same trematode species can affect host growth rate differently in closely-related snail species. The different level of antagonism between *M. piriformes* and two *Littorina* spp. may be attributed to generally lower resistance of *L. obtusata* to unfavourable environmental factors (K.V. Galaktionov, personal communication).

It is clear that each host–parasite combination is governed by its own rules, associated with ecological and physiological peculiarities of the snail and trematode species. Nevertheless, within the wide range of ecological, life cyclic, morphological and biological diversity of trematodes in general, *M. piriformes* and *M. pseudopygmaeus* should be considered as a very similar species. It is enigmatic, however, that these trematodes cause several types of host growth response: 'dwarfism' in *L. obtusata*, 'normal' growth in *L. saxatilis* and 'gigantism' in *O. aculeus*.

Why is the growth response of *Onoba* and *Littorina* to parasitic castration by 'pygmaeus' microphallides so different? The problem may be dealt with within the context of two concepts. Both operate with the life history of snail host and state that parasitic castration of a host forms the basis of the phenomenon, but produce quite different conclusions.

The first concept, proposed by Minchella (1985), is based on the idea that variations in the host life history in response to parasite infestation should be a common feature of any co-adapting host–parasite systems. By combining the hypothesis with previous results, Minchella (1985) predicts gigantism in parasitized individuals of long-lived (perennial) snail species. Negative effects of parasitism on host reproduction in such snails are short-lived relative to the maximum host's life. In contrast, in

short-lived (annual) host species gigantism should not be observed as a rule.

Whether or not the giant growth of infected snails may be considered as a 'coadaptive' phenomenon we leave out of the scope of this paper, because of the discussion on this subject is fruitless for understanding physiological mechanisms of the phenomenon. The most important point is the evident disagreement between data obtained in our study and predictions of Minchella's concept. *Onoba aculeus*, *L. saxatilis* and *L. obtusata* in terms of this concept should be attributed to 'perennial' species (>1.5 y). Nevertheless, only *Onoba* demonstrates gigantic growth following the infestation and *Littorina*, which survives in the field much longer, displays, either no growth alterations at all or even decreased growth rate.

The other concept, proposed by Sousa (1983), considers gigantism as a side, selectively neutral effect of parasitic castration and predicts it, in contrast to Minchella's (1985) hypothesis, in short-lived or semelparous snail hosts. Long-lived iteroparous species will rarely, if ever, exhibit enhanced growth following the infestation. In summary, Sousa's (1983) concept considering energy equilibrium in a host-parasite system takes into account the following factors that influence the snail growth response to infestation. First, the annual amount of energy invested in host breeding which is one of the parameters of the species life history. Second, the individual investment in breeding that varies with the individual host age. And finally, costs for host reparation of damages induced by parasitism determined by antagonism between host and parasite.

It seems that growth response of *Onoba* and both *Littorina* to infestation is in accordance with Sousa's (1983) prediction: the shorter-lived snail species exhibit gigantism in contrast to longer-lived ones. However, Sousa as well as Minchella (1985) defines upper longevity limit for 'short-lived' snails as 1.5 y; therefore it is not possible to attribute *O. aculeus* to those. This species in the White Sea can overwinter three times and survive up to about three years. It is worth noting that only two other known species with enhanced growth under infestation in the field, *Hydrobia ulvae* and *H. ventrosa* have very similar longevity ranges (Gorbushin, 1997). So, neither Minchella's (1985) nor Sousa's (1983) hypotheses are able to predict pronounced differences in growth response of *O. aculeus*, *L. saxatilis*, *L. obtusata*, *H. ulvae* and *H. ventrosa* to infestation with trematode parthenitae.

Mouritsen & Jensen (1994) observed another contradiction between these hypotheses: both authors use *H. ulvae* as an example of gigantism among short-lived (Sousa, 1983) and long-lived (Minchella, 1985) species. Gorbushin (1997) emphasized that, indeed, modern knowledge on life history of most of gastropod species is not good enough for an adequate comparative analysis. In our opinion, the consideration of life history variations as a key element in understanding the phenomenon should be performed within much wider longevity range than has been done previously. Actually, about 10% of *L. saxatilis* population on Ryazhkov Island (the White Sea) survive up to seven years (Granovitch, 1992). This fact and the finding in Kruglaya Bay (the White Sea) of the *L. littorea* having 17 clearly pronounced winter-grade lines on its shell (unpublished data) testify to a greater

diversity of snail life histories than both Minchella (1985) and Sousa (1983) recorded.

Developing Sousa's standpoint, Gorbushin (1997) supposed that, due to parasitism being one of the environmental factors which influence the host's condition, energy costs for struggling with parasites (Sousa, 1983) should be relatively high in adults of longer-lived species, in contrast to shorter-lived ones investing extensively into reproduction and sacrificing the effectiveness of reparative mechanisms. Hence, parthenitae of one and the same trematode species with wide specificity could be relatively more pathogenic for shorter-lived molluscs than for long-lived ones. Thus, despite the release of a large energy pool by parasitic castration in annual snail species, they do not show enhanced growth due to severe pathogenesis induced by parasites. Antagonism between the same parasite and a long-lived (>3–4 y) host is lower, however, parasitic castration due to relatively low reproduction effort does not release an energy pool large enough to provide additional growth. Gigantism as a trematode induced phenomenon would be expected in snail species having intermediate life history (longevity 2–3 y). The data presented in this paper is in accordance with the last hypothesis.

Other factors that are usually ignored when examining host-parasite interactions are elements of the physical and biotic environment where the interactions occur. The significance of environmental conditions in predetermination of snail growth response to trematode infestation was underestimated before Fernandez & Ecsh (1991). The authors postulated that variations in available energy to be shared between host and parasite should cause a different result in growth experiments using field and laboratory approaches. Indeed, Gorbushin (1997) has shown that host-parasite interactions across different environments may have different outcomes. Growth rates of *H. ulvae* infected with *Himasthla* sp. (Gorbushin, 1997) and *L. littorea* infected with *Renicola roscovita* (Mouritsen et al., 1999) may be different in different populations and habitats respectively. Growth responses of *H. ventrosa* to infestation with *Bunocotyle progenetica* may vary from normal to enhanced growth and decreasing population density (Gorbushin, 1997). However, due to behavioural alterations induced by parasites, spatial segregation of infected snails in the field hypothetically might lead to more or less successful feeding. The case exemplifying this idea has been described by Granovitch (1992) for *L. saxatilis* infected with 'pygmaeus' microphallides. These parasites influence the behaviour of the snails, interfering with their normal tidal migrations.

Thus, in field gastropod populations trematode parthenitae may significantly alter the host growth. Whether or not this phenomenon leads to any consequences for the host population is a problem that requires special consideration in each host-parasite combination. Another enigmatic point is the physiological mechanism of energy relocation in the snail-trematode system, which should be investigated in a laboratory using a multifactor approach.

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