

Infection patterns in White Sea blue mussels *Mytilus edulis* of different age and size with metacercariae of *Himasthla elongata* (Echinostomatidae) and *Cercaria parvicaudata* (Renicolidae)

K. E. Nikolaev, A. A. Sukhotin, K. V. Galaktionov*

Zoological Institute of the Russian Academy of Sciences, White Sea Biological Station, Universitetskaja Naberezhnaja 1,
199034 St. Petersburg, Russia

ABSTRACT: Infection of mussels *Mytilus edulis* L. by 2 trematode species was studied in a natural intertidal population in the Chupa inlet of the White Sea. The prevalence of metacercariae of *Himasthla elongata* (Mehlis, 1831) and *Cercaria parvicaudata* (Stunkard & Shaw, 1931) in mussels reached 100% in 3 to 4 yr old molluscs and remained at this level in older individuals. Infection intensity increased evenly with the age of the molluscan host, showing a tendency to decrease only in the oldest (9 yr old) mussels. These patterns of age dynamics of prevalence and infection intensity were associated with accumulation of trematode larvae in the course of the molluscs' lives. Ability of metacercariae to exist in mussels for long periods (at least 2.5 yr) was verified in the course of an experiment, during which infected molluscs were kept in a subtidal net cage. Decrease of infection intensity in the oldest individuals may reflect selective mortality of the most severely infected molluscs. Among mussels of the same age, higher infection intensity values occurred in larger individuals. This may be due to an enhanced pumping rate in large molluscs, which increases the probability of cercariae, free-living trematode larvae, infecting them via water currents.

KEY WORDS: Mussels · Metacercariae · Digenea · Age · Size · *Himasthla elongata* · *Cercaria parvicaudata* · White Sea

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INTRODUCTION

Trematode metacercariae parasitizing bivalve molluscs may influence vital functions of the hosts, lowering their resistance to unfavourable environmental factors and, in the case of intensive infection, even causing their death and resulting in mass mortality (Lauckner 1971, 1983, 1987, Bartoli 1974, James et al. 1977). Therefore, studies on bivalve-metacercariae interaction are very important, especially when applied to common and commercially important molluscan species. The blue mussel *Mytilus edulis* L. is one of the main components of intertidal and upper subtidal communities in the White Sea as well as being the object of an aquaculture industry in this region (Lukanin 1985, Sukhotin 1993). Five trematode species

have been reported from White Sea mussels; 2 of them, *Himasthla elongata* (Mehlis, 1831) (Echinostomatidae) and *Cercaria parvicaudata* Stunkard & Shaw, 1931 (Renicolidae), are the most common in molluscs inhabiting the intertidal zone (Chubrick 1966, Zelikman 1966, Kulatchkova 1985, 1987, Galaktionov 2001). Mussels are the second intermediate host for these 2 species of trematode, the first intermediate host being intertidal snails *Littorina* spp., and the final hosts being various species of marine and coastal birds such as gulls and waders.

The present work analyses the differential effects of host age and size on infection indices in mussels infected with *Himasthla elongata* and *Cercaria parvicaudata* metacercariae. Increase in prevalence and infection intensity with age and/or size of animal hosts

*Corresponding author. Email: gal@kg5910.spb.edu

is a well-established concept of ecological parasitology (Dogiel 1964, Kennedy 1975). Coincidentally, size and age are closely correlated in animals with asymptotic growth, including bivalve molluscs (Alimov 1981). Therefore, a change in physiological functions in the ontogenesis and, consequently, a change in infection indices could be due to an increase in size (linear size, volume, weight) of the organism, or an increase in age (i.e. ageing), or a joint impact of these 2 factors. Usually it is almost impossible to determine how these factors interact. However, in the White Sea intertidal zone, *Mytilus edulis* are exceedingly variable with regards to their growth rate (Savilov 1953, Sukhotin & Maximovich 1994). Molluscs in the 4 to 6 age groups may fall into the same size class, whereas mussels of the same age may differ in size significantly. This makes it possible to perform a differential analysis of the influence of mussel size and age upon changes in indices of infection with trematode metacercariae.

MATERIALS AND METHODS

Sampling. Blue mussels *Mytilus edulis* L. were collected in the intertidal zone of the cape dividing the Kruglaya and Seldyanaya creeks of the Chupa inlet (66° 20' N, 33° 40' E, Kandalaksha Bay, White Sea). This area of the White Sea is characterised by quite strong seasonal fluctuations in temperature and salinity. Throughout the year the temperature of the surface water fluctuates from –0.8 to 13.5°C, and the average salinity from 26.2 to 14.5‰ (Babkov 1998). Maximal tide amplitude is 2.0 to 2.1 m. The collection site was a rocky intertidal zone, with inclusions of pebbly-sandy areas. The lower and middle levels were densely covered with fucoids, mostly *Fucus vesiculosus* and *Ascochyllum nodosum*. Periwinkles *Littorina saxatilis* and *L. obtusata* were abundant there, whereas *L. littorea* was very rare. Numerous mussels (*Mytilus edulis*) covered the lower parts of the stones or formed separate druses. Population density of the molluscs was 3605 ± 21 ind. m⁻² (mussels with shell length exceeding 5 mm and of age 1 to 9 yr were considered).

Mussel samples (50 to 70 ind. per sample) were collected within the zone of fucoids in November 1999, March, August and November 2000, March and August 2001. The shell length of each mollusc was measured to the nearest 0.1 mm, and age was determined by counting lines of the winter growth stops on the shell. Only molluscs with shell length exceeding 5 mm were included in the analysis, because preliminary investigations demonstrated absence of metacercarial infection in juveniles younger than 1 yr. Mussels were dissected, their soft tissues squeezed between 2 slides and viewed under a stereomicroscope. The num-

ber of metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* localised in different mussel organs were counted. In metacercariae of *C. parvicaudata* 4 age groups were recorded, distinguished by their excretory bladder shape and the degree to which it was filled with excretory granules

- Young metacercariae (YM): a Y-shaped bladder that did not contain excretory granules
- Fully formed metacercariae (FFM): a bladder of regular Y-shape containing some excretory granules
- Old metacercariae (OM): a bladder of irregular shape occupying most of the metacercarial body and filled with numerous excretory granules
- Dead metacercariae (DM) in various stages of decomposition.

As the number of DM was small, they were not included in further analysis. We could not distinguish clear age groups in *Himasthla elongata* metacercariae.

Analysis. When calculating parameters of mussel infection with metacercariae, combined data from all samples were used. Prevalence (*P*) was calculated as the percentage of molluscs infected with a particular metacercarial species, and infection intensity (*IIn*) as the number of metacercariae of a particular species in an infected mussel.

When determining *P* with metacercariae in mussels of various sizes, 8 size (shell length) classes of molluscs were distinguished: I: 4.0–9.0 mm; II: 9.1–13.0 mm; III: 13.1–17.0 mm; IV: 17.1–21.0 mm; V: 21.1–25.0 mm; VI: 25.1–29.0 mm; VII: 29.1–33.0 mm; VIII: 33.1–37.0 mm. Mussel size effect on *IIn* was estimated by standard algorithms of regression and correlation analyses. Statistical significance of age influence upon *IIn* was determined using 1-way ANOVA (Underwood 1981). Post-hoc comparisons of *IIn* in mussels of different ages were performed with Tukey's test for unequal N. In some cases, Student's *t*-test was used for pair-wise comparison of means. All calculations were performed with the use of Statistica 5.5 software package.

To assess separate effects of mussel age and size on *IIn* with metacercariae of *Himasthla elongata* and FFM of *Cercaria parvicaudata*, 3 age groups of molluscs were distinguished: 1–3, 4–6 and 7–9 yr. For each age group linear regressions of *IIn* on mollusc size were computed. To assess the influence of age on the *IIn* of mussels with metacercariae, values of *IIn* from each mussel with *H. elongata* and *C. parvicaudata* larvae were corrected to the mean size of mussels in the sample (shell length *L* = 18 mm) according to the formula $IIn_{corr} = IIn + b(18 - L)$, where *IIn_{corr}* and *IIn* are corrected and observed infection intensity in a mussel, respectively, and *b* is the slope in linear regression of *IIn* on mollusc size for the corresponding age group (Table 1). For all mean values in the text and graphs, SEs are given.

Field experiment. To determine the life span of *Himasthla elongata* and *Cercaria parvicaudata* metacercariae, a field experiment was performed from December 2000 to August 2003. Mussels from artificial substrates of mariculture were used as initial material because no trematode infection was observed in them. Mussels are not infected in this habitat because cercariae shed by the intertidal snails *Littorina* spp. cannot reach mariculture substrates placed far from the shore (Fjälling et al. 1980, Kulatchkova 1985). To obtain cercariae, the first intermediate hosts of *H. elongata* and *C. parvicaudata*—periwinkles *Littorina saxatilis* and *L. obtusata*—were collected from the area of the intertidal zone where mussels were sampled. To distinguish between infected and non-infected snails, each individual was isolated in a dish and exposed to light for about 1 h. Snails shedding *H. elongata* and *C. parvicaudata* cercariae were isolated and used subsequently as a source of cercariae. Mussels collected from the mariculture substrates were each placed into a 70 ml vessel with seawater, and 10 to 15 cercariae of *H. elongata* or 30 to 35 cercariae of *C. parvicaudata* were added. Exposure time for molluscs was 8 to 10 h. After infection mussels were moved to a net cage, which was placed at some distance from the shore at a depth of 8 m. These conditions excluded the possibility of subsequent natural infection of experimental mussels. Once or twice a year (see Table 3), 6 to 7 molluscs were taken from the cage and examined for the presence of *H. elongata* and *C. parvicaudata* metacercariae by the same method as that used for mussels from natural settlement.

RESULTS

The metacercariae of *Himasthla elongata* in the mussels were always localised in foot tissues, whereas the larvae of *Cercaria parvicaudata* were found only in the liver. Average values of P for *H. elongata* and *C. parvicaudata* metacercariae in molluscs were very similar, $87.3 \pm 2.3\%$ and $91.6 \pm 2.4\%$, respectively. Average *IIn* with larvae of *C. parvicaudata* (25.3 ± 2.5) was much higher than that with *H. elongata* larvae (7.5 ± 0.6) ($p < 0.05$).

Metacercarial infection and host size

Both P and *IIn* of metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* in mussels depended on mussel size. P of metacercariae of *H. elongata* in the smallest mussels was $53.2 \pm 5.6\%$ and increased continuously with increasing host size, reaching 95 to 100% in large individuals (Fig. 1). The same tendency

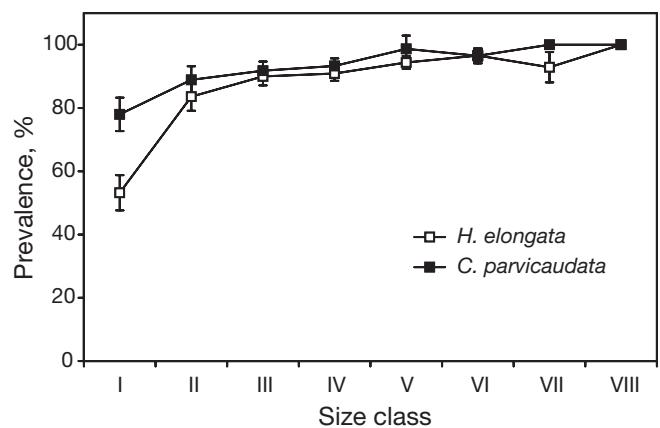


Fig. 1. *Mytilus edulis*. Prevalence of *Himasthla elongata* and *Cercaria parvicaudata* in mussels of different size

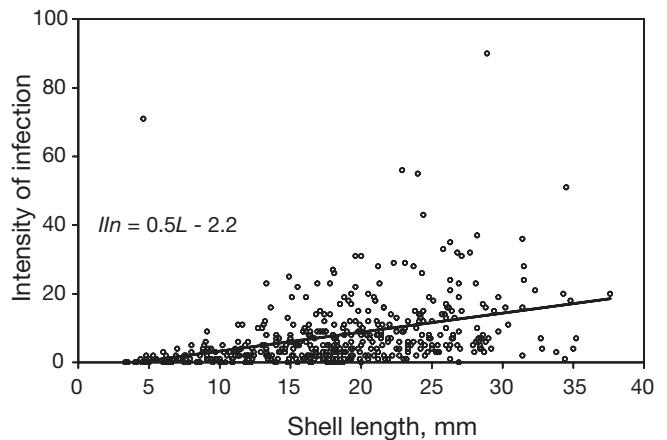


Fig. 2. *Mytilus edulis*. Intensity of infection (*IIn*) with *Himasthla elongata* metacercariae in mussels of different size (*L*)

was observed for P of *C. parvicaudata* metacercariae in mussels (Fig. 1), P in mussels in Size Class I reaching $78 \pm 5.3\%$.

The *IIn* with *Himasthla elongata* metacercariae also increased significantly with increasing size of mussels ($R = 0.404$, $n = 455$, $p < 0.001$) (Fig. 2). Dependence of *Cercaria parvicaudata* *IIn* on host size differed in metacercariae of different age groups. In YM *IIn* was relatively constant, increasing slightly though significantly in the largest mussels ($R = 0.197$, $n = 455$, $p < 0.001$) (Fig. 3A). The number of FFM per host specimen increased greatly with the host's increasing size, reaching more than 50 metacercariae per ind. in the largest mussels ($R = 0.469$, $n = 455$, $p < 0.001$) (Fig. 3B). In comparison with the total number of larvae from other age groups, the number of OM was insignificant in mussels of all size classes (average *IIn* 1.4 ± 0.2), and grew slightly with increasing size of mussels ($R = 0.299$, $n = 455$, $p < 0.001$) (Fig. 3C).

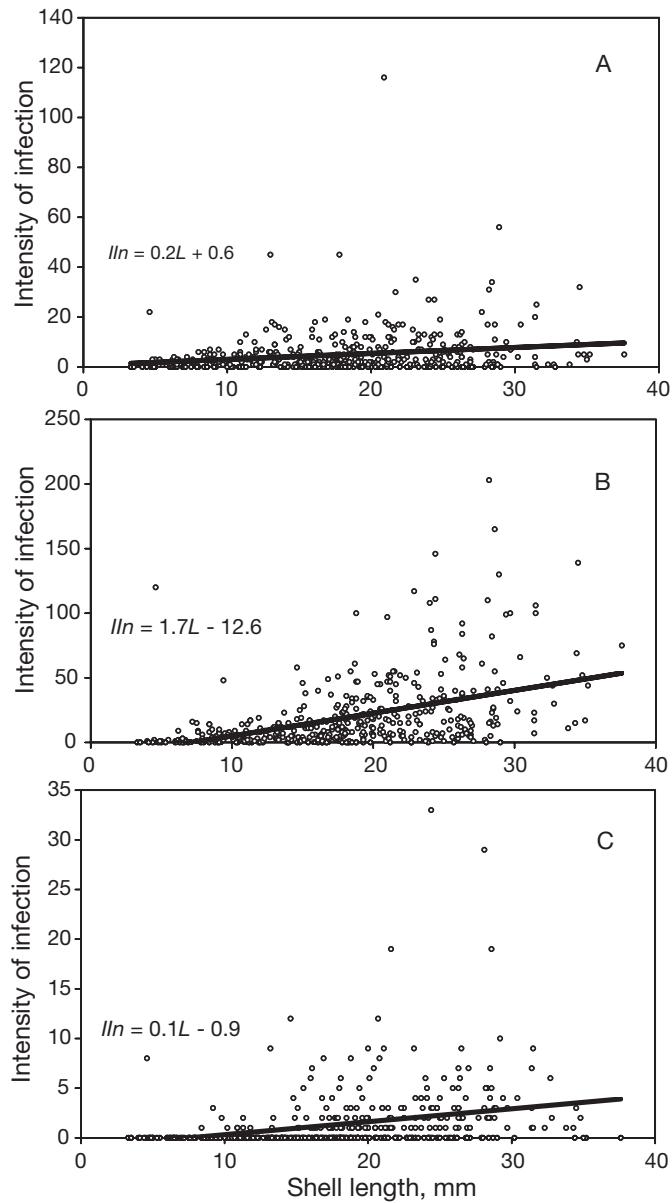


Fig. 3. *Mytilus edulis*. IIn with *Cercaria parvicaudata* metacercariae of different age groups of mussels of different size (L). (A) Young metacercariae (YM); (B) fully formed metacercariae (FFM); (C) old metacercariae (OM)

Metacercarial infection and host age

Dependence of P of *Himasthla elongata* metacercariae on age of mussels was asymptotic (Fig. 4). As mussels aged, P increased continuously, reaching $91.8 \pm 2.7\%$ in 4 yr old mussels and tending to level off afterwards (Fig. 4). Age dynamics of P of *Cercaria parvicaudata* metacercariae in mussels was similar (Fig. 4). It is noteworthy that there was a decrease in P in 2 yr old mussels as compared to 1 yr old ones ($p < 0.05$, Tukey's HSD test). It was followed by an increase

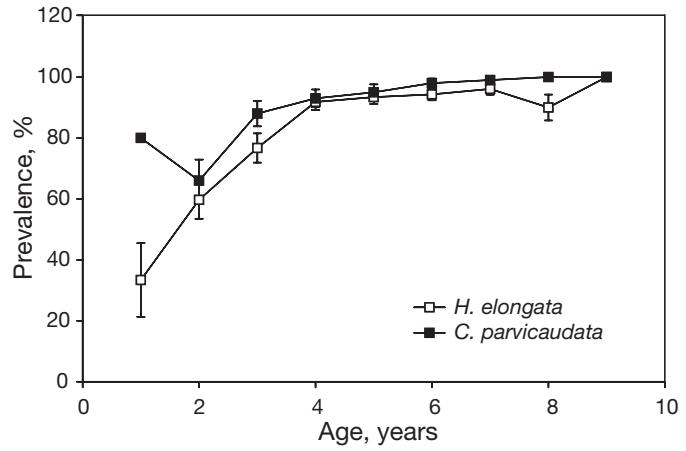


Fig. 4. *Mytilus edulis*. Prevalence of *Himasthla elongata* and *Cercaria parvicaudata* in mussels of different age

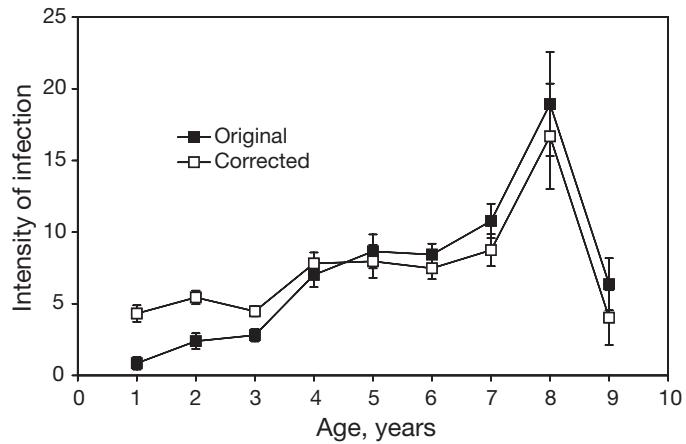


Fig. 5. *Mytilus edulis*. Original and size-corrected IIn with *Himasthla elongata* metacercariae in mussels of different ages

in P up to $88 \pm 4.2\%$ in 3 yr old specimens. In older mussels, P did not vary significantly.

Mussel age considerably influenced IIn with metacercariae of *Himasthla elongata* (ANOVA, < 0.001). With increasing host size, IIn increased from 0.8 ± 0.3 in 1 yr old mussels to 10.7 ± 1.0 in 7 yr and 18.9 ± 2.5 in 8 yr old mussels. However, in the oldest (9 yr old) mussels, the value of this index fell to 6.3 ± 1.4 ($p = 0.025$, Tukey's HSD test) (Fig. 5).

The host age effect on IIn with *Cercaria parvicaudata* larvae was similar among metacercariae of different age groups. IIn with YM was relatively low (4.9 ± 0.4) and increased until the host reached 8 yr (ANOVA, $p < 0.01$). In 9 yr old mussels an insignificant tendency for a decrease in IIn with YM was observed (Fig. 6); however, sample size (15 ind.) was too small for meaningful statistical analyses. The number of FFM increased with increasing age of the hosts (ANOVA, $p <$

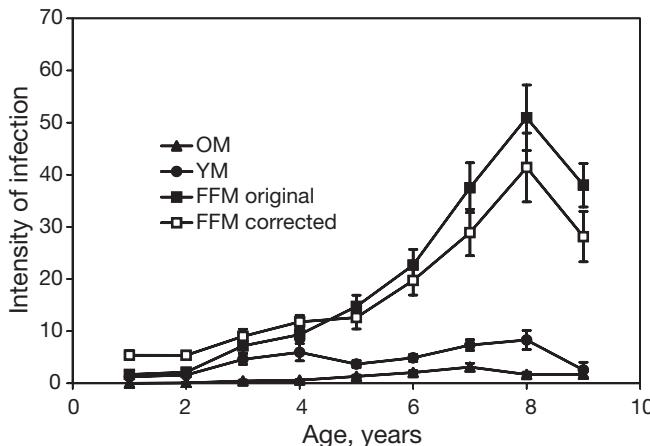


Fig. 6. *Mytilus edulis*. Original and size-corrected *IIn* with *Cercaria parvicaudata* OM, YM and FFM metacercariae in mussels of different ages. Size-corrected *IIn* with FFM also presented

0.001), reaching its maximum in 8 yr old individuals (50.9 ± 6.2 metacercariae per ind.). In 9 yr old mussels, an insignificant decrease in *IIn* with this age group of metacercariae was also observed. Although the number of OM was low, it also increased significantly from 0 in 1 yr old mussels to 3.1 ± 0.7 in 7 yr old mussels (ANOVA, $p < 0.01$), decreasing down to 1.6 ± 0.4 and 1.7 ± 0.5 in 8 and 9 yr old individuals, respectively (Fig. 6).

Differential influence of size and age of mussels on metacercarial infection

Within each of the 3 mussel age groups, the influence of molluscan hosts age on *IIn* with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* was statistically significant (Table 1). The only exception was *IIn* with *H. elongata* larvae in the oldest age group of the mussels. An increase in *IIn* with increasing size of mussel was recorded in all age groups.

The effect of age on *IIn* of mussels corrected to average size (18 mm) with metacercariae of *Himasthla elongata* and FFM of *Cercaria parvicaudata* was significant (ANOVA, $p < 0.001$ for both trematode species) (Table 2, Figs. 5 & 6). An abrupt increase in *IIn* with age was observed in mussels older than 3 and 6 yr in the case of *H. elongata* infection, and in mussels older than 5 yr in the case of *C. parvicaudata* infection.

Results of the field experiment

All control dissections of the experimentally infected mussels from the cage revealed the presence of

Table 1. *Mytilus edulis*. Influence of mussel host age on intensity of infection (*IIn*) with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata*. Parameters of regression equation $IIn = a + bL$ for mussels of different age groups. L : shell length of mussels (mm), a and b : coefficients of the regression equation, R : correlation coefficient, N : number of mussels analyzed

Mussel age	<i>a</i>	<i>b</i>	<i>R</i>	<i>p</i>	<i>N</i>
<i>H. elongata</i>					
1–3	-1.329	0.343	0.530	<0.001	116
4–6	0.155	0.421	0.285	<0.001	232
7–9	4.293	0.353	0.139	ns	106
FFM of <i>C. parvicaudata</i>					
1–3	0.604	0.365	0.231	<0.05	116
4–6	-8.273	1.295	0.330	<0.001	232
7–9	5.714	1.493	0.233	<0.050	106

Table 2. *Mytilus edulis*. 1-way ANOVA results of influence of age on *IIn* of mussels with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata*. *IIn* values were corrected for mean length of mussels (18 mm)

	SS	df	MS	<i>F</i>	<i>p</i>
<i>H. elongata</i>					
Age	3795.6	8	474.4	6.35	0.000
Error	33318.3	446	74.7		
FFM <i>C. parvicaudata</i>					
Age	45065.5	8	5633.2	11.37	0.000
Error	221063.1	446	495.7		

Table 3. *Mytilus edulis*. Mean number of metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* in mussels that were experimentally infected in December 2000 and kept in subtidal cage

Date of observation	Mean number of metacercariae		
	<i>H. elongata</i>	<i>C. parvicaudata</i>	
	YM	FFM	OM
21 Mar 2001	9	1	25
14 Aug 2001	8	0	32
12 May 2002	7	0	15
26 Aug 2002	10	0	29
15 Aug 2003	8	0	22
			1

Himasthla elongata and *Cercaria parvicaudata* metacercariae in numbers comparable with the initial number of cercariae used for infection (Table 3). In the very first sample of mussels from the cage, taken 3 mo after the beginning of the experiment, all metacercariae of *C. parvicaudata* were at the FFM stage. In later samples, only accumulation of excretory granules in the bladder was observed. OM and DM were absent throughout the experiment (Table 3), and so were decomposing metacercariae of *H. elongata*.

DISCUSSION

Almost all mussels in the studied settlement were infected with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata*. This is typical for intertidal mussel settlements in the Kandalaksha and Onega Bays of the White Sea, which indicates that conditions for parasite transmission are favourable there (Kulatchkova 1985, 1987, Galaktionov 2001, our unpubl. data). The P of rediae and sporocysts of *C. parvicaudata* in the first intermediate hosts, the periwinkles, at the sampling site of mussels was approximately the same throughout the investigation period, and did not exceed 1 to 2% (our unpubl. data). Therefore, a statistically significant higher *IIn* of mussels with metacercariae of *C. parvicaudata* cannot be explained by a higher prevalence of this species in the first intermediate hosts. It is very likely to be associated with much higher productivity of intramolluscan stages of *C. parvicaudata* compared with that of *H. elongata*. Average daily emission of *H. elongata* cercariae from infected *Littorina littorea* was 642 ± 22 (438 to 1002 ind.), and that of *C. parvicaudata* cercariae 2266 ± 122 (1053 to 3404 ind.), the larvae of the latter species retaining infectivity for a longer time (V. Prokofiev pers. comm.). Thus, even if *IIn* in the first intermediate hosts was the same, the average density of *C. parvicaudata* cercariae in a separate area of the intertidal zone turned out to be much higher than that of *H. elongata* cercariae. This increased the chances of the cercariae of the latter species infecting the second intermediate host, mussels.

The data obtained demonstrate a significant dependence of mussel infection with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* on age and size of the molluscan host. The growth of P is observed only in younger mussels, whereas mussels older than 3 or 4 yr exhibit an almost 100% P of larvae of the 2 trematode species studied. At the same time, *IIn* increases evenly with increasing age of the molluscan host, tending to decrease only in the oldest individuals. These patterns of age dynamics of P and *IIn* appear to be associated with accumulation of metacercariae throughout the mussel's life.

The life span of trematode metacercariae is very long. It reaches 7 to 8 mo in the larvae of Fasciolidae and Notocotylidae that encyst on submerged substrates, while the highly specialised metacercariae of Diplostomidae retain infectivity in the second intermediate host for up to 5 or 6 yr (Dönges 1969). According to our experiments, metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* live for at least 3.5 yr, the larvae of *C. parvicaudata* not reaching the state of OM during this period. It would therefore seem that the life span of metacercariae of both trematode species is limited by that of infected mussels. This suppo-

sition is supported, in particular, by the low number of OM and DM of *C. parvicaudata* in mussels of all ages. Dead metacercariae of *Renicola roscovita* and *H. elongata* in North Sea cockles were recorded by Lauckner (1983) mostly in spring. However, in that case, high mortality of metacercariae was not a result of the action of internal defence systems of molluscs; the larvae encysted in the tissue of palps died due to freezing.

High P of *Cercaria parvicaudata* metacercariae in mussels of age 1+ and its decrease in 2 yr old mussels is likely caused by elimination of severely infected individuals under unfavourable conditions, e.g. in winter months. The most infected molluscs are the first to die. This premise is corroborated by the fact that *IIn* in 2 yr and 1 yr old mussels is almost the same, varying within the range of 1 to 2. A similar pattern was described in juvenile *Cerastoderma edule* infected with metacercariae of *Renicola roscovita* and *Himasthla elongata* in the North Sea (Lauckner 1983). Most of the highly infected cockles of the 0-group died during their first winter, and the average *IIn* of the molluscs inspected in the following spring was lower than that of specimens settled in the previous autumn. Probably, at least in the White Sea, *C. parvicaudata* metacercariae are more pathogenic to young mussels than larvae of *H. elongata*, whose values of P and *IIn* in mussels did not decrease in 2 yr old individuals.

As well as in young specimens, a decrease in the *IIn* with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* was observed in the oldest mussels (9 yr) (Figs. 5 & 6). Although in the case of *C. parvicaudata* this decrease was not statistically proven (possibly due to the small sample size), visual observations showed a difference in infection between 8 and 9 yr old individuals. In the case of *H. elongata* this pattern was highly significant. Maximal longevity of mussels in the White Sea intertidal populations does not exceed 10 yr (Savilov 1953, Sukhotin et al. 2003). The 9 yr old animals are already rare and 10 yr old mussels are exceptional. Since 9 yr old mussels are approaching the maximal lifespan, it is likely that the negative impact of parasitizing metacercariae may be greater in the oldest, weakest individuals. This may result in selective mortality of the most infected specimens due to the influence of unfavourable environmental factors (decreasing water salinity in spring, winter frosts on the intertidal zone, long-term air exposure etc.). Therefore, only the less-infected mussels remain alive. In addition, a decreased prevalence in the old mussels could be due to immune factors. Mussels in the research area were shown to be heterogeneous with regard to the degree of manifestation of non-specific defence mechanisms in response to penetration of cercariae of the studied trematode species (Gorbushin & Levakin 2005). The population consists of individuals

with different resistance to cercarial infection. It may be suggested that only the most resistant, and thus the most poorly infected, specimens live to older age (although no non-infected 8 or 9 yr old mussels were found).

Besides age, size also considerably influences infection intensity in mussels with metacercariae: among mussels of the same age, the highest I_{ln} values are observed in larger individuals. Cercariae of the species studied enter the mantle cavity of the molluscan hosts passively in water currents via the inhalant siphon (Stunkard 1964, Loos-Frank 1967, Werding 1969, Lauckner 1983, de Montaudouin et al. 1998, Wegeberg et al. 1999, our observations). Therefore, the influence of host size upon I_{ln} with metacercariae of *Himasthla elongata* and *Cercaria parvicaudata* may be mediated by the pumping rate of mussels. Pumping rate in bivalve mussels directly depends on the size of the animal (Winter 1978, Alimov 1981, Jørgensen 1990). Thus, increased pumping activity of mussels may increase the probability of their infection with trematode larvae.

As a corollary, in the host-parasite systems under consideration (mussels and metacercariae of *Himasthla elongata* and *Cercaria parvicaudata*), the infection indices of the molluscan hosts are determined by both their age and their size. Similar results were obtained by Bowers & James (1967), who studied infection of the cockles *Cardium edule* by metacercariae of *Meiogymnophallus minutus* on the South Wales coast. A higher I_{ln} in large juveniles of *Cerastoderma edule* compared to that in smaller ones was noted by de Montaudouin et al. (1998). A similar pattern may be characteristic of other host-parasite systems involving a long-living parasite, if the latter is not highly pathogenic to the host and if the probability of infection correlates positively with the host's size (in our case, this was mediated by pumping rate).

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