



Substratum preferences in two notocotylid (Digenea, Notocotylidae) cercariae from *Hydrobia ventrosa* at the White Sea



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ABSTRACT

Notocotylids are digeneans with a two-host life cycle. Their cercariae encyst on underwater substrata, and final hosts (mostly water birds) get infected by consuming encysted metacercariae. The aim of this study was to assess whether notocotylid cercariae have encystment substratum preferences. We used *Cercaria Notocotylidae* sp. No 11 Deblock, 1980 (presumably *Paramonostomum alveatum* Mehlis 1846) and *C. Notocotylidae* sp. No 12 Deblock, 1980 associated with mudsnails *Hydrobia ventrosa* at the White Sea. Three series of experiments were performed in which distribution of cysts across different combinations of substrata was measured. The results suggest that *C. Notocotylidae* sp. No 11 cercariae encyst almost exclusively on the leaves of green plants without any plant species preferences. *C. Notocotylidae* sp. No 12 cercariae use shells of living molluscs and plant substrata equally often but avoid empty shells. These preferences are probably adapted to the feeding habits of the final hosts and this may enhance the transmission of the studied notocotylid species. Mechanisms of the observed preferences might be associated with the ability of cercariae to recognize substrata features: either chemical cues or surface structure. Substratum selectivity in cercariae is considered as a first step towards downward incorporation of the second intermediate host into the life cycle.

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1. Introduction

The role of cercariae in the complex life cycle of digeneans is transmission of infection from the first intermediate host to the second intermediate or the final host. In Plagiorchhiida with a two-host life cycle, such as Paramphistomoidea, Pronocephaloidea, Fasciolidae, Psilostomidae and Haplospalchnidae, upon leaving the molluscan host cercariae encyst on underwater substrata, becoming metacercariae (the next larval stage). The final hosts get infected by eating substrata with encysted larvae. There is evidence that cercariae from different taxa have certain substratum preferences which may facilitate trophic transmission of infection via herbivore–vegetation and predator–prey links (for review see Pearson, 1972; Cribb et al., 2003). For instance, digenean cercariae parasitizing herbivores as adults (e.g. Paramphistomoidea, some Pronocephaloidea and Fasciolidae) mostly encyst on vegetation. If the final hosts are predators, cercariae tend to encyst on their potential prey. For example, cercariae of some Philophthalmidae encyst on snail shells and those of Haplospalchnidae, on planktonic organisms (Pearson, 1972; Prinz et al., 2011; Neal and Poulin, 2012). Echinostomatidae and Psilostomidae demonstrate a wide range of

preferences: encystment in water, encystment on the surface and in the cavities of hydrobionts (e.g. gill cavity or surface) and penetration into hosts' tissues, that is, true endoparasitism (Fried, 2001; Cribb et al., 2003; Galaktionov and Dobrovolskij, 2003). There is a tendency towards transition from the use of animals as cercarial encystment substrata to their use as second intermediate hosts and thus the formation of the three-host life cycle.

Notocotylids lack the second intermediate host. Their cercariae may encyst on different underwater substrata such as molluscan shells, aquatic invertebrates, vegetation and stones (Pearson, 1971; Khalifa and El-Nafar, 1978; Garkavi, 1968; Dönges, 1962; Odening, 1966; Besprozvannykh, 2010; Alekseev, 1962; Skirnisson et al., 2004; Kulachkova, 1954). Encystment inside the mollusc's mantle cavity is also known (Filimonova, 1985). At least some notocotylids appear to select a certain substratum type for encystment (Pearson, 1972). Understanding substratum specificity in the cercariae of these two-host digeneans may provide an insight into the sequence of events resulting in the incorporation of the second intermediate host into the digenean life cycle. However, the available data on notocotylid substratum preferences are scarce and not statistically tested. Additionally, it remains unclear how strict the choice of the preferred substratum may be.

The aim of our study was to investigate substratum preferences, if any, in cercariae of two notocotylid species common in the White Sea.

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The intramolluscan stages of these trematodes are associated with intertidal mudsnails *Hydrobia* spp.

2. Materials and methods

2.1. Notocotylid species

Species identification of notocotylid cercariae is quite difficult (Filimonova, 1985; Barton and Blair, 2005). According to earlier studies, a single notocotylid species (*Paramonostomum alveatum*) occurs in mudsnails at the White Sea (Kulachkova, 1954). However, our preliminary study has shown that at least 3 notocotylid species use *Hydrobia ulvae* and *Hydrobia ventrosa* snails as the first intermediate host at the White Sea. Morphologically these cercariae correspond, respectively, to *Cercaria Notocotylidae* sp. No 11, *C. Notocotylidae* sp. No 12 and *C. Notocotylidae* sp. No 13 as described by Deblock (1980) from the coasts of France. The species status of these larvae is also confirmed by sequencing results (ITS1, Cox1 and 18S rDNA D1 domain markers) (Gonchar, unpublished).

Given the existing data on host species, locality, morphology and preliminary experimental infections (Kulachkova, 1954; Stunkard, 1966, 1967a; Deblock, 1980; Skirnisson and Galaktionov, 2014), we can suppose that *C. Notocotylidae* sp. No 11 probably belongs to *P. alveatum* and *C. Notocotylidae* sp. No 13 to *Notocotylus atlanticus* Stunkard, 1966. *C. Notocotylidae* sp. No 12 is morphologically similar to cercariae of *Uniserialis breviserialis* (now considered synonymous to *Notocotylus skrjabini*) as described by Stunkard (1967b) in *Hydrobia salsa* on the Atlantic coast of the USA around Woods Hole, Massachusetts. There is no experimental evidence to confirm that *C. Notocotylidae* sp. No 12 belong to *N. skrjabini*. *C. Notocotylidae* sp. No 13 infection in the White Sea hydrobians is rare. Therefore in this study we focused on cercariae of the two abundant species, *C. Notocotylidae* sp. No 11 and *C. Notocotylidae* sp. No 12.

2.2. Sampling site and procedure, selection and maintenance of infected mudsnails

The research was carried out at the White Sea Biological Station of the Zoological Institute of the Russian Academy of Sciences (66°20' N, 33°38' E) in August in 2011–2014. Mudsnails *H. ventrosa* were collected at the intertidal site Levin Navolok, Chupa Inlet (Kandalaksha Bay of the White Sea). The mud samples were washed in the laboratory through a sieve with a 1-mm² mesh to recover snails of average to large size (shell length ~3 mm). Smaller snails have a low infection prevalence (our observations). The snails were kept in the laboratory at 4 °C in containers filled with natural seawater and fed with filtered sludge and rubbed filamentous algae. In order to promote shedding of cercariae and thus detect infected molluscs, snails were placed individually in the wells of 24-well plates with seawater and exposed to sunlight for 2 h. The snails from the wells containing either cercariae or freshly encysted metacercariae of notocotylids were used in experiments as a source of cercariae. Snails infected with two or more digenean species were excluded from this study. Cercariae morphotype was identified on temporary mounts under the stereomicroscope (105× and 420×).

2.3. Experimental design

To test substratum preferences we put one infected snail and experimental substrata in a 40 mm plastic Petri dish with 4 ml of natural seawater, covered by two microscope slides. The dishes were kept at 20 °C and a constant even illumination (fluorescent lamp) for 24 h – conditions favourable for cercariae emergence (our observations). We have chosen to place an infected snail rather than pre-collected cercariae into the experimental dishes because water disturbances caused by pipetting cercariae trigger immediate non-specific encystment (previous observations). All the resulting cysts (encysted metacercariae)

were then counted. Prior to the experiment the snail shells were cleared of any preexisting notocotylid cysts.

A total of three experimental series were performed. The initial series was a trial one. The following series were planned based on its results. In the first experimental series (e1.1 and e1.2) both cercariae of *C. Notocotylidae* sp. No 11 and *C. Notocotylidae* sp. No 12 were offered a variety of potential substrata (objects that snails may come across in their natural habitat) in order to identify their possible range. These substrata were distributed, evenly and somewhat overlapping, between the two subseries: e1.1 (n = 114; living molluscs *H. ventrosa*, *H. ulvae* and *Littorina saxatilis*, seagrass *Zostera marina*, meadow *Poa* sp. and a stone) and e1.2 (n = 35; living molluscs *H. ventrosa*, *Onoba aculeus* and *Mytilus edulis*, seagrass *Z. marina*, brown algae *Fucus vesiculosus* and a piece of dead wood). In the second experimental series (e2) we limited substrata options to two and used cercariae of *C. Notocotylidae* sp. No 11 (n = 66) and *C. Notocotylidae* sp. No 12 (n = 78) separately. In the third experimental series cercariae of *C. Notocotylidae* sp. No 11 (e3.1; n = 42) and *C. Notocotylidae* sp. No 12 (e3.2; n = 46) cercariae were offered different ranges of potential substrata. In all experiments similarly-sized substrata were used. The snails occupied random position in the dish and the leaves were secured in the centre.

2.4. Statistics

The variable used in the statistical analysis was the percentage of cysts on a certain substratum from the total number of cysts on all experimental (i.e. excluding the dish surface) substrata within a particular dish. The data were arcsine-transformed and comparisons were made with a *t*-test and Chi-square test (e3.2). Dishes with less than 5 cysts on experimental substrata were excluded from the analysis.

3. Results

In each experimental series some cysts were found on the dish surface. Their amount relative to the dish surface area was insignificant. Out of the numerous potential substrata tested in the first experimental series (e1.1, n₁ = 114, and e1.2, n₂ = 35; Table 1), stone and wood were found to bear almost no cysts. Encystment on various plant substrata (*Z. marina*, *Poa* sp., *F. vesiculosus*) was notable. Some shells were also widely used (*H. ventrosa*, *M. edulis*), while few cysts were found on other shells (*L. saxatilis*, *O. aculeus*). The substrata with more cysts, namely the shell surface and seagrass *Z. marina*, were tested in the second experimental series (e2).

Cercariae of *C. Notocotylidae* sp. No 11 and *C. Notocotylidae* sp. No 12 demonstrate different patterns of cysts distribution between these two simple experimental substrata. *C. Notocotylidae* sp. No 11 cercariae encyst almost exclusively on grass (*t*-test $p < 0.001$, n = 66, Fig. 1).

Table 1

Mean rates of cysts of *C. Notocotylidae* sp. No 11 and ssp. No 12 (combined) on different substrata (e1).

	Substratum	Mean % of cysts ± SE
e1.1 (n ₁ = 114)	Hven	4.6 ± 0.26
	Hulv	2.0 ± 0.23
	Lsax	0.47 ± 0.09
	Zmar	51.58 ± 0.53
	Poa	21.33 ± 0.39
	Stone	0.35 ± 0.1
e1.2 (n ₂ = 35)	Hven	11.05 ± 2.7
	Oacu	1.8 ± 0.53
	Medu	10.94 ± 1.9
	Zmar	21.58 ± 2.22
	Fves	13.55 ± 2
	Wood	0.26 ± 0.4

Hven, *H. ventrosa* shell; Hulv, *H. ulvae* shell; Lsax, *L. saxatilis* shell; Zmar, *Z. marina* leaf; Poa, *Poa* sp. leaf; Stone, stone surface; Oacu, *O. aculeus* shell; Medu, *M. edulis* shell; Fves, *F. vesiculosus* thallus; Wood, dead wood surface; n₁, number of tests in e1.1; n₂, number of tests in e1.2.

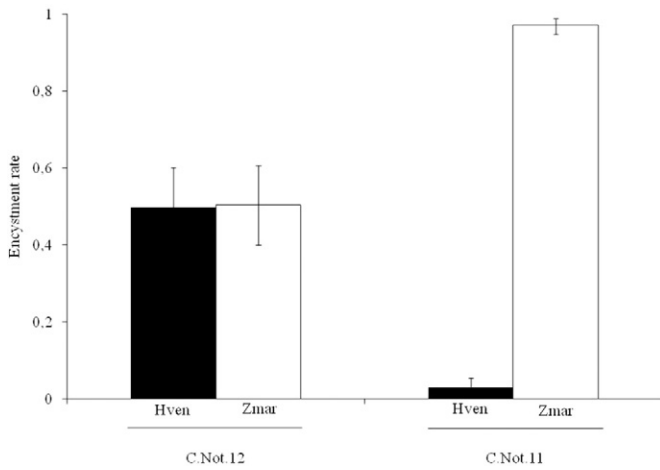


Fig. 1. Rates of notocotylid cercariae encystment on two alternative substrata (e2). C.Not.12, *C. Notocotylidae* sp. No 12; C.Not.11, *C. Notocotylidae* sp. No 11; Hven, *H. ventrosa* shell surface (black bars); Zmar, *Z. marina* leaf surface (white bars); vertical bars represent confidence intervals (95%).

C. Notocotylidae sp. No 12 cysts are equally numerous on shells and grass (t-test $p = 0.94$, $n = 78$, Fig. 1).

The third experimental series tested cercariae of *C. Notocotylidae* sp. No 11 with two alternative plant objects as possible substrata (e3.1; *Z. marina* and *Poa* sp.) and cercariae of *C. Notocotylidae* sp. No 12 – with a variety of shell substrata (e3.2; *H. ventrosa* host individual, uninfected *H. ventrosa*, *H. ulvae*, empty *H. ventrosa* shell). In e3.1 *C. Notocotylidae* sp. No 11 cercariae have shown no preference when exposed to *Z. marina* and *Poa* sp. (t-test $p = 0.42$; $n = 42$, Fig. 2). *C. Notocotylidae* sp. No 12 cercariae in e3.2 virtually did not encyst on empty shell surfaces (0.8% of cysts) but were distributed evenly across the shells of different living snails ($n = 46$; $\chi^2 = 0.012$; $p = 0.99$) (Fig. 3).

4. Discussion

Our results indicate that cercariae of two notocotylid species abundant in costal ecosystems of the White Sea have certain substratum preferences. Notocotylid cercariae exhibit an “active searching” behaviour, with fast movement and a strong photo-reaction (Prokofiev and Galaktionov, 2009). As a result, some substrata are clearly avoided (e.g., stones or pieces of wood). This avoidance can apparently be explained by the low likelihood of metacercariae reaching the final host using such substrates.

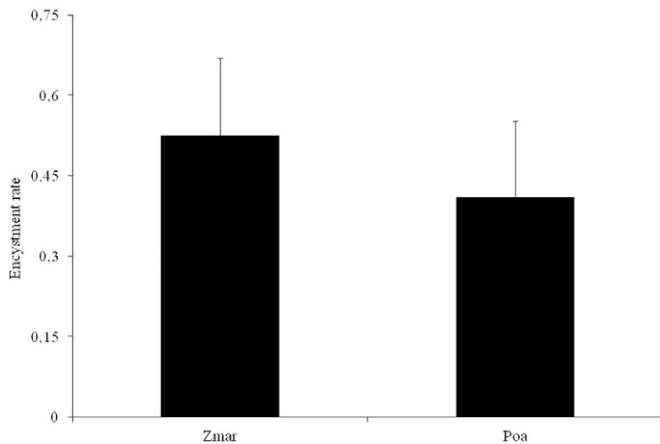


Fig. 2. Rates of *C. Notocotylidae* sp. No 11 cercariae encystment on alternative vegetal substrata (e3.1). Zmar, *Z. marina* leaf surface; Poa, *Poa* sp. leaf surface; vertical bars represent confidence intervals (95%).

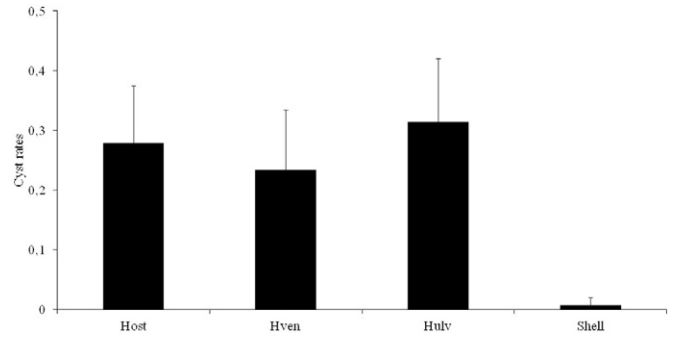


Fig. 3. Rates of *C. Notocotylidae* sp. No 12 cercariae encystment on various shell substrata (e3.2). Host, *H. ventrosa* host individual’s shell surface; Hven, *H. ventrosa* uninfected individual’s shell surface; Hulv, *H. ulvae* shell surface; Shell, surface of an empty *H. ventrosa* shell; vertical bars represent confidence intervals (95%).

Molluscan shells and plant leaves were shown to be potential encystment substrata for studied notocotylid species. However, the great diversity of substrata inside one dish in the trial experiment e1 made it impossible to identify exact preferences. Further experiments showed clearly that cercariae of *C. Notocotylidae* sp. No 11 had a strong bias towards plant substratum, with almost no cysts on the shell surface. As for cercariae of *C. Notocotylidae* sp. No 12, they encysted on the host shell as readily as on the green leaves of *Z. marina*.

There is evidence in the literature that notocotylid cercariae of closely related species may prefer different substrata for encystment. For example, *Notocotylus ralli* cercariae never encysted on plant substratum in a laboratory setting, forming cysts only on hard and smooth surfaces: the vessel walls and the shells of living molluscs (Dönges, 1962; Odening, 1966). According to Dönges (1962), the latter is used as the major substratum used by *N. ralli* cercariae in the natural environment also. At the same time, *Notocotylus imbricatus* cercariae, though behaving similarly to those of *N. ralli*, encyst much more readily on water plants (*Elodea canadensis* and *Lemna minor*) which the ducks are known to feed on (Dönges, 1962). *Notocotylus attenuatus* metacercariae were experimentally shown to occur in large numbers on freshwater shrimps’ cuticle in the Russian Far East, mainly on the gills and gill covers (Alekseev, 1962). This substratum enhances transmission of a parasite via food webs, favours its dispersal and prevents the drying of the cysts. Unfortunately, these and other accounts of notocotylid preferences in encystment substratum available in literature (reviewed in Pearson, 1972; Filimonova, 1985) are purely descriptive, with no statistically inferred data provided. Such data are available for Philophthalmidae cercariae which also encyst in the open. Both field and laboratory findings suggest that *Philophthalmus* sp. from New Zealand mudsnails *Zeacumantus subcarinatus* prefer to encyst on the shells of several snail species rather than on seaweed, other molluscs and crustaceans (Neal and Poulin, 2012).

As noted in the Introduction section, the adaptive nature of such preferences is that it increases the probability of successful transmission to the vertebrate host (Pearson, 1972). At the White Sea adults of *P. alveatum* (*C. Notocotylidae* sp. No 11 here) were recorded in common eiders *Somateria mollissima* (see Kulachkova, 1954). At the White Sea this duck feeds mostly on invertebrates, including snails and mussels (Bianki et al., 1979; Krasnov et al., 2009). This seems to contradict our finding about the preferred encystment of cercariae of *C. Notocotylidae* sp. No 11 on grass. However, *P. alveatum* has also been reported from multiple species of ducks, swans and even some sandpipers (Filimonova, 1985). Some of these birds, such as swans and several ducks, are grass feeders, while others, including the common eider, can accidentally consume vegetation while feeding on animals. Our data show that the final hosts of *C. Notocotylidae* sp. No 12 are waterfowl feeding on benthic invertebrates and occasionally eating plants (e.g. diving ducks).

It should be noted that, although some encystment substrata are clearly preferred over the other, none of them is an exclusive option

for the notocotylid cercariae studied. All the objects tested throughout the current study, both living and non-living, had at least one cyst recorded on their surface. Moreover, we have observed instances of non-specific encystment on experimental dish and water surface. This indicates that any existing substrate specificity is not strict.

The observed patterns of cyst distribution on different substrata cannot yet be explained conclusively. Cercariae recognize the host by chemical cues such as fatty acids, cholesterol, triacylglycerols etc. (reviewed in Haas, 2003). No such data exist for cercariae encysting in the open, but most probably suitable substrata are also recognized by chemical cues. Another possibility is identification of the substratum by its structural features. From what has been observed for *C. Notocotylidae* sp. No 12 cercariae, it seems that something in a living mollusc attracts the cercariae, regardless of the molluscan species and the presence or absence of infection. Perhaps they can mechanically detect whether the shell surface is covered with conchiolin. At the same time, cercariae of *C. Notocotylidae* sp. No 11 and *C. Notocotylidae* sp. No 12 recognize sea grass *Z. marina* and land grass *Poa* sp. as a suitable encystment substratum, possibly relying on a chemical cue shared by the green plants. The structure of leaf surface is different in these two species, suggesting that it might be of no importance for substratum recognition by the studied notocotylid cercariae.

5. Conclusions

Our data clearly demonstrated that cercariae of notocotylids associated with the White Sea mudsnails can select encystment substrata. Apparently, this ability is inherent in cercariae of most, if not all, notocotylids (for review see Filimonova, 1985). It does not mean favouring a particular substratum (e.g. one or several close species of plants) but rather a group of similar substrata (e.g. water vegetation) that are most likely to be eaten by final hosts. The same broad “specificity” towards encystment substratum is characteristic of other digenean larvae that form cysts in the open (for review see Pearson, 1972; Cribb et al., 2003). It is likely to be associated with the recognition of chemical cues common for a broad range of possible encystment substrata. The ability to select substratum in a way that increases the chance of trophic transmission can be seen as a first step to a downward incorporation of a second intermediate host into the life cycle. This happened independently in different digenean taxa and was followed by the establishment of both morphological (penetration glands, stylet, virgule etc.) and behavioural (host-searching, host-recognition, penetration) adaptations in cercariae (Cribb et al., 2003; Dobrovolskij and Galaktionov, 2003; Galaktionov and Dobrovolskij, 2003).

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