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Research Article

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The natural history of *Echinorhynchus bothniensis* Zdzitowiecki and Valtonen, 1987 (Acanthocephala) in a high Arctic lake

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Abstract: The acanthocephalan *Echinorhynchus bothniensis* Zdzitowiecki and Valtonen, 1987 differs from most other species in the genus *Echinorhynchus* Zoega in Müller, 1776 by infecting mysids (order Mysida) instead of amphipods (order Amphipoda) as intermediate hosts. Here we report on the occurrence of *E. bothniensis* in mysids (*Mysis segerstralei* Audzijonytė et Väinölä) and in its fish definitive hosts in a high Arctic lake. Out of 15 907 sampled mysids, 4.8% were infected with a mean intensity of 1.05 worms (range 1–5), although there was notable variation between samples taken in different years and sites. Larger mysids appear more likely to be infected. Of five fish species sampled, charr, *Salvelinus alpinus* (Linnaeus), and a benthic-feeding whitefish morph, *Coregonus lavaretus* (Linnaeus), were the most heavily infected (mean abundances of 80 and 15, respectively). The adult parasite population in fish exhibited a female-biased sex ratio (1.78 : 1). Although *E. bothniensis* is rather unique in infecting mysids, many aspects of its natural history mirror that of other acanthocephalan species.

Keywords: body size, Echinorhynchidae, intermediate host, *Mysis*, sex ratio, thorny-headed worms

Mysids (order Mysida) are known to be the intermediate hosts of some trophically-transmitted helminths (Smith and Lankester 1979, Prychitko and Nero 1983, Marcogliese and Burt 1993), including the acanthocephalans *Echinorhynchus bothniensis* Zdzitowiecki et Valtonen, 1987 and *E. leidy* Van Cleave, 1924. These acanthocephalans differ from their close relatives by using mysids and not amphipods as intermediate hosts (Schmidt 1985). Valtonen et al. (1983) found that amphipods could be infected with eggs from female acanthocephalans from Baltic cod, *Gadus morhua* Linnaeus, which were later identified as *E. gadi* Zoega in Müller, 1776, whereas experimental infection of amphipods with eggs of acanthocephalans from smelt, *Osmerus eperlanus* (Linnaeus), failed.

This led Zdzitowiecki and Valtonen (1987) to describe the acanthocephalans from smelt in the northern part of the Bothnian Bay as a new species, *E. bothniensis*. Using allozymes, Väinölä et al. (1994) confirmed that *E. bothniensis* was genetically distinct from other species of *Echinorhynchus* Zoega in Müller, 1776 in northern Europe. Valtonen and Crompton (1990) found *E. bothniensis* in 14 fish species, although it matured in only six of these, most commonly smelt and burbot, *Lota lota* (Linnaeus). Here, we report the occurrence of *E. bothniensis* in its intermediate and definitive hosts in a high Arctic lake, Lake Pul-

mankijärvi, with the goal of describing the natural history of this species and comparing it to other acanthocephalan species. A cursory description of some of these data were reported by Aura et al. (1990) in a conference abstract.

MATERIALS AND METHODS

Study site

Lake Pulmankijärvi is a high Arctic, oligotrophic lake on the border between Finland and Norway (69°59'N; 28°00'E). Its size is 12.1 km², with a mean and maximum depth of 6.7 and 34 m, respectively. Waters flow to the Arctic Ocean via the Pulmankijoki and Tenojoki rivers. It lies 14 m above sea level with steep shores. The most common fish species are pelagic- and benthic-feeding forms of whitefish, *Coregonus lavaretus* (Linnaeus), grayling, *Thymallus thymallus* (Linnaeus), three-spined stickleback, *Gasterosteus aculeatus* Linnaeus, minnow, *Phoxinus phoxinus* (Linnaeus), and, as a peculiarity, a flatfish, *Platichthys flesus* (Linnaeus), which migrates from the Arctic Ocean. Other fish species occurring in the lake are Arctic char, *Salvelinus alpinus* (Linnaeus), brown trout, *Salmo trutta* Linnaeus, salmon, *S. salar* Linnaeus, nine-spined stickleback, *Pungitius pungitius* (Linnaeus), pike, *Esox lucius* Linnaeus, perch, *Perca fluviatilis* Linnaeus, burbot and rarely eels, *Anguilla anguilla* (Linnaeus) (Niemelä and Hynninen 1983).

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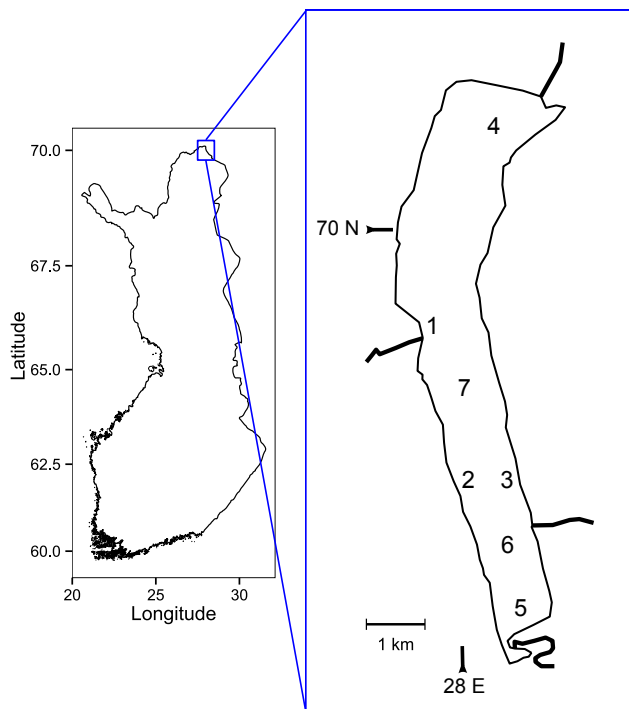


Fig. 1. Map of Lake Pulmankijärvi with sampling sites (right). The inset on the map of Finland (left) shows the location of the study lake. Site 7 is the deepest point in the lake (34 m).

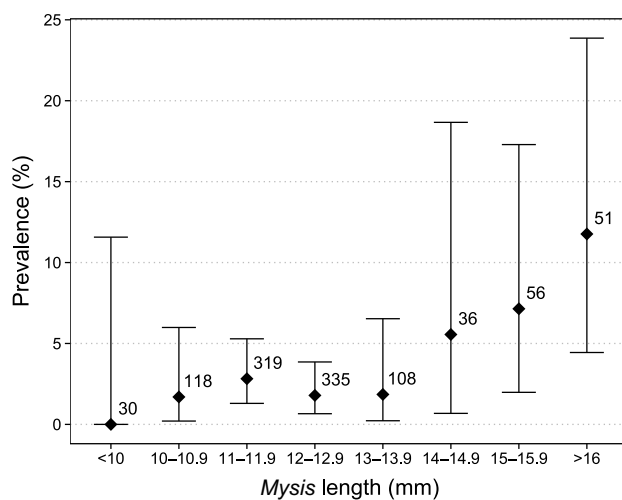


Fig. 2. The prevalence of *Echinorhynchus bothniensis* Zdzitowiecki and Valtonen, 1987 in mysids of different sizes collected in June 1989. Sample sizes in each group are indicated and bars represent the 95% CI.

Sampling of intermediate hosts

Mysis segerstralei Audzijonytė and Väinölä (formerly *M. relicta* Lovén, see Audzijonytė and Väinölä 2005) were collected in 1984, 1985, and 1989 from 7 sites in Lake Pulmankijärvi (Fig. 1, Table 1). Benthic samples were collected with a trawl net as well as an Ockelman-type bottom sledge (both having a mesh size of 0.6 mm). The nets were pulled along the lake bottom for a few minutes to collect mysids. Additionally, bongo nets (2 connected sieve-nets with a height of 2 m, an opening of 60 cm in diameter, and a mesh size of 0.3 mm) were used to collect mysids from the water column at known depths, and a pull net (surface area

Table 1. Samples of *Mysis segerstralei* Audzijonytė et Väinölä taken from Lake Pulmankijärvi and examined for infection with *Echinorhynchus bothniensis* Zdzitowiecki et Valtonen, 1987.

Sample	Sites	Depth (m)	N	Prevalence (%)	Worms	Max intensity
Jun 1984	1-3	11-30	470	0	0	-
September-October 1984	1-3	5-30	1057	0.28	3	1
July 1985	4	5-15	3220	4.66	160	5
July 1985	5	15-17	2152	11.20	246	2
July 1985	6	25-30	4099	5.03	220	4
July 1985	7	34	3046	3.18	100	2
June 1989	7	34	1053	2.94	32	1
Total	-	-	15097	4.82	761	5

N – number of mysids examined; worms – acanthocephalans recovered.

of 1 m² and a mesh size of 0.4 mm) was used to sample the entire water column. Mysids collected with different devices were combined to calculate infection parameters for one site at one time. The size of the mysids in the 1989 sample was measured to the nearest 1 mm. Recovered acanthocephalans were stained using Grenacher borax carmine, dehydrated in an alcohol series, cleared in beechwood oil, and embedded in Canadian balsam. Subsamples of worms were sexed and measured.

Sampling of fish

In June 1989, five fish species were caught with gill-nets and frozen. The intestinal tract of thawed fish was examined later in the laboratory. Acanthocephalans were identified to species and females were recorded as non-gravid (just ovarian balls) or gravid (mature acanthors present). Terminology conforms to that proposed by Bush et al. (1997).

RESULTS

Echinorhynchus bothniensis in mysids

We found 761 individuals of *E. bothniensis* in 15097 *Mysis segerstralei* (Table 1). Prevalence varied between samples. From the near-coast sites sampled in 1984, only 3 infected mysids were collected (0.2%), whereas a maximum prevalence of 11.2% was obtained at one site in 1985. Most of the infected mysids harboured a single worm (overall mean intensity = 1.05); the maximum intensity was 5. In the 1989 sample, the prevalence of infection differed significantly between size groups (Chi-square test, $\chi^2_7 = 21.78$, $P = 0.003$), and appeared to increase in larger mysids (Fig. 2).

For 619 worms sexed in the 1985 samples, the male to female sex ratio was 1.14 : 1, which did not differ significantly from an equal sex ratio (Chi-square test, $\chi^2_1 = 2.72$, $P = 0.099$). Female cystacanths ($n = 74$, mean = 4.59 mm, range = 3.38–6.25 mm) were longer than males ($n = 67$, mean = 3.53 mm, range = 2.75–4.38 mm). The sexual development of these cystacanths was relatively advanced. The females had up to 150 ovarian balls free in the body cavity (mean = 100, $n = 40$, range = 60–150). In male larvae, the average testis length was 0.43 mm ($n = 64$, range 0.26–0.64 mm), which is only about 33% smaller than the typical testis size for adults in this population (Wayland 2013).

Table 2. Infection of *Echinorhynchus bothniensis* Zdzitowiecki et Valtonen, 1987 in five fish species sampled in June 1989 from Lake Pulmankijärvi. The proportion of males, females with just ovarian balls (non-gravid), and females with at least some shelled acanthors (gravid) was calculated for each host except the flatfish.

Fish species	Fish length (mm) (SD)	N	Prevalence (%)	Total worms recovered	Males : non-gravid females : gravid females (%)
<i>Coregonus lavaretus</i> (Linnaeus) (pelagic)*	156 (17)	36	8.3	6	50 : 33 : 17
<i>Coregonus lavaretus</i> (Linnaeus) (benthic)*	238 (36)	30	70	456	40 : 35 : 25
<i>Salvelinus alpinus</i> (Linnaeus)	189 (51)	9	100	721	33 : 24 : 43
<i>Thymallus thymallus</i> (Linnaeus)	238	4	25	3	67 : 33 : 0
<i>Platichthys flesus</i> (Linnaeus)	158	4	50	14	-

*the mean number of gill rakers differs between pelagic- and benthic-feeding forms of whitefish and was 40 and 25, respectively.

Echinorhynchus bothniensis in fish

Both of the two coregonids were infected, but *E. bothniensis* was far more common in the benthic-feeder (Table 2, mean abundance: 15.2 vs 0.2). Although only 9 char were examined, the high prevalence (100%) and mean intensity of infection (80) suggests that this may be an important definitive host for *E. bothniensis* in Lake Pulmankijärvi. Mature females were also found in grayling and flounder (Table 2). The overall sex ratio of parasites collected from fish was significantly biased towards females (1.78 females for each male, Chi-square test, $\chi^2_1 = 92.9$, $P < 0.001$).

DISCUSSION

Within the genus *Echinorhynchus*, *E. bothniensis* and the closely related *E. leidy* are exceptional, using mysids instead of amphipods as intermediate hosts (Prychitko and Nero 1983, Valtonen et al. 1983). Ours is the first study on the ecology of *E. bothniensis* in its intermediate host. Prevalence was low overall (4.8%) and typically just one worm was recovered per infected mysid. E.T. Valtonen (unpubl. data) observed a similar prevalence (1.3%) and intensity of infection (1.1) in mysids ($n = 1397$) from Lake Keitele in central Finland, and Prychitko and Nero (1983) found *E. leidy* at prevalences up to 3.6% in North American mysids. These prevalences are comparable to those for species of *Echinorhynchus* infecting amphipods (e.g. *E. gadi*: 0.8% – Marcogliese 1994, 0.9% – Benesh et al. 2015, *E. salmonis* Müller, 1784: 8.8% – Nybelin 1924, 0.1% – Amin 1978, 0.9% – Okaka 1984, 0.4% – Benesh et al. 2015, *E. truttae* Schrank, 1788: 2.3% – Okaka 1984, 2.8% – Lassiere 1989, 4.1% – MacNeil et al. 2003, 1.3% – Dezfuli et al. 2008). Thus, it is not obvious that acanthocephalan transmission to and/or from mysids and amphipods differs substantially.

Prevalence in mysids varied between samples, but this might be attributable to spatial (differences between sites or depths) or temporal effects (differences between years). In any case, this variation could contribute to the aggregated distribution of adults in fish (Valtonen and Crompton 1990). We also found higher prevalence in larger mysids. An increase in infection with intermediate host size has been observed in other acanthocephalans (Liat and Pike 1980, Wilson and Hubschman 1985, Lagrue et al. 2007, Oliva et al. 2008, La Sala et al. 2012), although peak abundances in medium-sized hosts is perhaps the more common pattern (Hine and Kennedy 1974,

Muzzall 1978, 1982, Camp and Huizinga 1980, Bratney 1986, Brown and Pascoe 1989, Lagrue et al. 2007, Outreman et al. 2007, Rauque and Semenas 2007). A number of processes could result in higher prevalence in bigger mysids. For example, bigger mysids may be older and thus have had more time to be exposed to infection, or small, infected mysids might have higher mortality rates than large, infected mysids. An elevated mysid growth rate caused by *E. bothniensis*, such that infected mysids quickly become large, is also a possibility, but it seems less likely, given that acanthocephalans sometimes have little impact on intermediate host growth (Uznanski and Nickol 1980, Benesh and Valtonen 2007a).

In the intermediate host, females of *E. bothniensis* have well-developed ovarian balls and males have large testes, particularly relative to their body size, indicating that this species reaches an advanced state of maturity as larvae (Crompton 1985). Sexual size dimorphism is also clear in the intermediate host, which is common for species of *Echinorhynchus* – see Benesh and Valtonen (2007b). The sex ratio of *E. bothniensis* was slightly and non-significantly male-biased in mysids, but strongly female-biased in fish. This suggests that recruitment into and/or loss from each host may differ between the sexes. In acanthocephalans displaying seasonality, adult sex ratios often become more female-biased over the course of a season, suggesting that females survive longer than males (e.g. Tedla and Fernando 1970, Valtonen 1980, Bratney 1988, Lasee 1989). This probably explains the over-representation of females of *E. bothniensis* in our fish samples. Alternatively, the manipulation of host phenotype can also differ between male and female cystacanths (Benesh et al. 2009), hinting at the possibility of sex-specific transmission rates from intermediate to definitive host. However, the nearly equal sex ratio in larval *E. bothniensis* is not consistent with females having a substantially higher transmission rate out of mysids and into fish compared to males.

In Lake Pulmankijärvi, Arctic char and benthic-feeding coregonids were the main definitive hosts of *E. bothniensis*. This acanthocephalan was described from smelt (Zdzitowiecki and Valtonen 1987), but mature females have also been found in lampreys, burbot, flounder, and salmonids like trout and whitefish (Valtonen and Crompton 1990). Thus, it appears to have a wide definitive host range. The low abundance in plankton-feeding whitefish suggests that mysid consumption, rather than the host's phylogenetic affinities, is a key determinant of infection in fish.

Väinölä et al. (1994), using allozymes, found that *E. bothniensis* from Lake Pulmankijärvi differed genetically from worms collected from two locations in the Baltic Basin (Bothnian Bay and Lake Keitele, Central Finland), although they did not consider the divergence sufficient to deem them separate species. Morphological differentiation between these two genetic groups of *E. bothniensis* is limited (Wayland 2013). The mysids found in these two areas

have now been recognised as separate species (Audzijonytė and Väinölä 2005), which hints at co-evolution between these worms and their mysid hosts, although additional analyses would be needed to robustly test this hypothesis.

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