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Academic Dissertation

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Abstract

The life-cycles of two *Rhipidocotyle* species and their ecology at different life-cycle stages, especially the host-parasite relationships in the first intermediate host, were studied during 1987-89 in Lake Saravesi, central Finland, and Lake Kuivasjärvi, northern Finland. At the beginning of the study, bucephalid digeneans were found in *Rutilus rutilus* and adult bucephalids of the genus *Rhipidocotyle* were found in predatory fishes from Lake Saravesi. However, two bucephalid species, the cercariae of the first having long, filamentous furcae (Type A) and the second having short, stout furcae (Type B), were detected in *Anodonta anatina* from the lake. Experimental life-cycle studies on the parasites had to be established, in which uninfected roach were infested with a known type of cercaria and the roach were fed to uninfected *Esox lucius* or *Perca fluviatilis*. Type B was revealed to be *R. campanula* (Dujardin, 1845). Type A also belonged to the genus *Rhipidocotyle*, being a species new to science and was described under name *R. fennica* Gibson, Taskinen & Valtonen, 1992. Both species used *A. anatina* as the first intermediate host and *R. rutilus* as the second intermediate host. The final hosts of *R. fennica* and *R. campanula* were *E. lucius* and *P. fluviatilis*, respectively. The metacercariae of *R. fennica*, which mainly occurred encysted in the skin and fins of *R. rutilus*, could be distinguished by the more psterior position of the pharynx along the body when compared to *R. campanula* which, on the other hand, mainly occurred encysted in the gills of *R. rutilus*. Adult *R. fennica* could be separated from *R. campanula* e.g. by its smaller egg size and more posterior position of the anterior margin of the vitelline fields.

The prevalences of *R. fennica* and *R. campanula* in *A. anatina* from Lake Saravesi (n=1,157) were 33.2 % and 1.0 %, respectively. *Pseudanodonta complanata* (n=29), *Unio tumidus* and *U. pictorum* (n=65) from Lake Saravesi were not infected. The prevalence of *R. campanula* in *A. anatina* from Lake Kuivasjärvi (n=1,486) was 4.7 % and *R. fennica* did not occur in that lake. *A. anatina* collected from Lake Saravesi ranged from 1 to 15 years and from 21 to 112 mm. The clam specimens ≤ 3 years or ≤ 51 mm were not infected with *R. fennica*. The prevalence of *R. fennica* in *A. anatina* from Lake Saravesi was higher in the littoral zone, among older, bigger, fast growing and female clams.

The emergence of *R. fennica* cercariae began during July and continued throughout September. In the laboratory the maximum duration of *R. fennica* cercarial emergence was 72 days. The emergence of *R. campanula* cercariae in Lake Kuivasjärvi occurred from as early as mid-June until mid-August, although the lake is more northernly situated. The cercarial emergence of both species coincided with the development of the glochicia larvae in the uninfected clams. *R. fennica* cercariae emerged mainly during the day whereas that of *R. campanula* occurred mainly at night. The daily production of *R. fennica* and *R. campanula* cercariae was on the average 9,500 and 1,400 specimens, respectively. However, the life span of *R. fennica* cercariae was shorter ($\bar{x}$ 17 hours) than that of *R. campanula* ($\bar{x}$ 28 hours).

The proportion of heavily infected clams among the infected ones was higher (90 %) for *R. campanula* than for *R. fennica* (30 %) infections, which indicates a higher pathogenity of *R. campanula* to *A. anatina* as compared with *R. fennica*. This may contribute to the lower prevalences of *R. campanula* observed in both lakes. Branched sporocyst tubules of both species were mainly located in the gonads of the clams. This, and the coincidence of cercarial production with the reproduction of the (uninfected) clams, are viewed as behavioural adaptions of the parasites to obtain as much energy from the host as possible with minimal negative effects on host survival.

Both *Rhipidocotyle* species frequently filled the gonad and, in advanced infections, spread through almost all tissues of the clam. It could be estimated that every third female clam from the littoral zone of Lake Saravesi was unable to reproduce because of *R. fennica* infection. This, and other potential consequences of *Rhipidocotyle* infections, should be taken into account when *A. anatina* individuals, populations or communities which they participate, are studied.

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List of original publications

The thesis is based on the following articles, which will be referred to by their Roman numerals:

I Taskinen, J., Valtonen, E. T. & Gibson, D. I. 1991: Studies on bucephalid digeneans parasitising molluscs and fishes in Finland. I. Ecological data and experimental studies. - Systematic Parasitology 19: 81-94.

II Gibson, D. I., Taskinen, J. & Valtonen, E. T. 1992: Studies on bucephalid digeneans parasitising molluscs and fishes in Finland. II. The description of *Rhipidocotyle fennica* n. sp. and its discrimination by principal component analysis. - Systematic Parasitology 23: 67-79.

III Taskinen, J., Mäkelä, T. & Valtonen, E. T. 1992: Bucephalid digeneans of *Anodonta anatina* in two Finnish lakes. I. Seasonality of infection and cercarial emergence in relation to the reproduction of the host. - Manuscript (submitted).

IV Taskinen, J., Valtonen, E. T. & Mäkelä, T. 1992: Bucephalid digeneans of *Anodonta anatina* in two Finnish lakes. II. Location and quantity of sporocysts and seasonality of developmental stages. - Manuscript (submitted).

V Taskinen, J. & Valtonen, E. T. 1992: Age-, size- and sex-specific infection of *Anodonta anatina* (Mollusca: Unionidae) with *Rhipidocotyle fennica* (Trematoda: Bucephalidae) and its influence on host reproduction. - Manuscript (submitted).

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Contents

1. Introduction

Digenean trematodes using molluscs as intermediate hosts can have profound effects on components of the aquatic ecosystem (Lauckner, 1986). The function of the whole ecosystem may change because (1) a reduction in the breeding potential by "parasitic castration" may result in serious declines or fluctuations in host populations, and (2) species-specific infestation by trematodes can lead to changes in faunal composition and, therefore, in the structure of community and entire ecosystem. Wikgren (1952) observed replacement of a dominant gastropod species by another one due to a trematode infection in brackish-water shore pools of the Baltic Sea. In addition, as an important grazer on benthic algae, *Littorina littorea* is a key species in intertidal communities, having an important habitat-modifying effect (Lubchenco & Menge, 1978; Lubchenco, 1983; Bertness, 1984). The trematode-related mortality of larger *L. littorea* in areas of an excessive development of algal mats was found to be in excess of 90 % during summer, which may account for algal explosions in the area studied by Lauckner (1986). Furthermore, digeneans of molluscs can change the community and ecosystem structure by affecting their second intermediate host populations. *Hydrobia* spp. snails have microphallid trematodes, which utilize small crustaceans as the second intermediate hosts. Muus (1967) reported an almost total late-summer breakdown of the population of *Corophium volutator*, a key species among the littoral crustaceans, due to *Hydrobia* -borne larval microphallids in Danish waters. Corophiids are major food items of flatfish, and their destruction by trematodes causes serious consequences for fish stocks (Muus, 1967).

In Europe, the introduced mussel, *Dreissena polymorpha*, is a well-known biofouling organism that can disrupt the water treatment operations and electricity generating facilities (Afanas'yev and Protasov 1987), it also may negatively affect native mollusc populations (Arter 1989), and alter the nutrient and energy flow of aquatic ecosystems (Stanczykowska *et al*. 1976; Shevtsova and Kharchenko 1981; Stanczykowska and Planter 1985; Kharchenko and Lyashenko 1985; Hamburger, Dall & Jonasson, 1990). According to Reeders, Vaate & Slim (1989), *D. polymorpha* had a capacity to filter the volume of two Dutch lakes once or twice a month and to have a remarkable effect on the phytoplankton communities and trophic status of the lakes. *D. polymorpha*

was also the most important food source for wintering diving ducks (Vaate, 1991). *D. polymorpha* has recently invaded North American lakes. By settling on the shells of native clams *Dreissena polymorpha* interferes their metabolism having capacity to reduce the population size or even eliminate it (Mackie 1991). *D. polymorpha* was introduced into Lake St. Clair in 1986 and spread through Lake Erie in three years (Griffiths *et al.*, 1991). Strayer (1991), is of the opinion that *D. polymorpha* could spread throughout of North America. A bucphalid trematode *Bucephalus polymorphus* occur in *D. polymorpha* (Baturo 1977). Potential negative effects of *B. polymorphus* on the survival and reproduction of *Dreissena polymorpha*, the parasite may have a significant role in many water ecosystems.

Through age- and size-dependent infection and parasite-induced host mortality the trematodes may modify the size and age distributions of their molluscan hosts. Reliable growth curves and equations - essential in quantitative ecology - cannot be extracted from such disorted size-frequency distributions (Lauckner, 1986). Trematodes may also have an impact on the host response to environmental factors; Vernberg & Vernberg (1963) have demonstrated, for example, a reduced resistance to high temperatures in infected snails *Nassarius obsoletus*.

The ecological consequences of digenean infestations in molluscs can also include interference with host-biomass, production and turnover-rate estimations by by-passing of host-assimilated energy. In advanced infestations, the entire digestive gland and gonad of a mollusc may be replaced by parasites. Lauckner (1986) states that in a dense and highly infested marine mollusc population the biomass of trematodes may amount to tons of weight along some strips of coastline. In addition, the cercariae of trematodes liberated from a mollusc may remove a remarkable amount of material and energy from the host during a short time. For example, Howell (1966) reported up to 10,000 *Bucephalus longicornutus* cercariae emerging from an infected oyster *Ostrea lutaria* in 24-hours.

While having serious negative effects on the survival and reproduction of the host (e.g. Lauckner 1983), the digenean trematodes can be expected to have a strong impact on the evolution of their molluscan host species.

According to Howell (1966), the life cycle of digeneans belonging to the family Bucephalidae is complex, involving three parasitic and two free-living phases. The adults are generally intestinal parasites of predatory fish. They produce eggs which hatch in water (or possibly within the rectum of the host) liberating free-swimming miracidia. These are small, pear-shaped organisms, and unique among trematodes in that the ciliae are borne on rod-like appendages. If they penetrate a suitable bivalve mollusc they develop into long, branched sporocysts in the visceral organs. Germinal cells in the sporocyst wall are proliferated into the sporocyst lumen and give rise to cercariae which are characterised by

long, contractile furcae, (von Baer, 1827). After liberation from the sporocyst the cercariae commence a short free-living phase which culminates in attachment, penetration and encystment to form a metacercaria in the skin of the fish 2nd intemediate host. When infected fish are eaten by predatory fish the metacercariae excyst and develop into sexually mature adults (Howell, 1966).

The bivalve mollusc *Anodonta anatina* L. (=*A. piscinalis* Nilsson) belongs to the family Unionidae. The freshwater Unionidae of the temperate zone reproduce annually (Ellis, 1978). Reproduction can be divided temporally into two stages: (1) gemetogenesis and embryogenesis, leading to the development of glochidia larvae in the clam; and (2) release of the glochidia and invasion into the host fish, where the glochidia metamorphose. The glochidia of *A. anatina* are attached to fish for less than four weeks (Ellis, 1978; Jokela, Valtonen & Lappalainen, 1991), and they can infect several host species (e.g., Jokela *et al*. 1991). *A. anatina* can consititute up to 95 % of the zoobenthic biomass of a lake (Ökland, 1963) and it can have a significant impact on lake nutrient cycling (Kasprzak, 1985; Nalepa, Gardner & Malzcyk, 1991). It has been used in environmental monitoring (e.g. Eriksson, Meriluoto & Lindholm, 1989; Herve, 1990) and in developing the theory of life history evolution (Haukioja & Hakala, 1978a).

The host-parasite relationship between molluscs and digeneans has been studied quite widely in snails (Gastropoda), especially concentrating on the trematodes causing human diseases. However, the dynamics of bivalve-trematode associations has received much less attention. A good example of the scarcity of studies on bivalves and their digenean parasites can be found in the digenean family Bucephalidae, the subject of the present study. Although Yamagati (1958) recognized 145 species of adult bucephalids parasitising marine and freshwater fishes, only few cercariae and metacercariae have been reported, and experimental life-cycle studies have been carried out on only five marine species (see Lauckner, 1983) and on four freshwater species (Woodhead, 1929; Kniskern, 1952; Baturo, 1977).

At the same time the life-cycles of most bucephalid species are unknown and detailed studies on host-parasite relationships of bucephalids are very few. Baturo (1977) studied the seasonality of the prevalence and cercarial emergence of *Rhipidocotyle campanula* and *Bucephalus polymorphus* in *Dreissena polymorpha*, *Unio pictorum* and *Anodonta* sp. in two Polish lakes 1972-73. She found *B. polymorphus* in *D. polymorpha* with prevalences of 0.6 % and 2.4 %. No bucephalids were found in *Anodonta* sp. but in *Unio* sp. from one of the lakes *R. campanula* occupied 3.2 % of the clams. The prevalence of *R. transversale* and *R. lintoni* in *Lyosina hyalina* and of *Cercaria bucephalopsis haimeana* in *Cardium edule* in relation to the age and size of the host has been studied by Stunkard

(1976) and Bowers (1969), respectively. Bucephalid digeneans have been reported to cause castration of their bivalve hosts (e.g. Kniskern, 1952; Tripp, 1973; Stunkard, 1976; Lauckner, 1983; Wardle, 1988; Wardle, 1990). The effect of *C. bucephalopsis haimeana* on the growth rate of *C. edule* has been studied by Bowers (1969). Bucephalid parasites can affect also the fish communities, since they have been found to cause mass mortality in their fish hosts (Hoffmann et al., 1990).

They only previous records of bucephalids in Finland are those of Järnefelt (1921), who claimed to have found *B. polymorphus* in 1.2 % of *Perca fluviatilis* in Tuusulanjärvi in southern Finland, and Hakala (1979), who studied eight *Anodonta* populations in southern Finland and found *Bucephalus* sp. in prevalences varying from 0-50 % in different populations. The species of bucephalid actually found by these authors is, however, questionable. It would have not been possible for Järnefelt to distinguish *B. polymorphus* from *R. campanula* in 1921. In the standard identification manual of the time, that of Lühe (1909), the figure said to be *B. polymorphus* clearly resembles *R. campanula*. In view of the present results, Hakala's identification based on larval material must also be doubtful.

In European freshwater fishes two common species of trematodes of the family Bucephalidae, known as *Bucephalus polymorphus* Baer, 1827 and *Rhipidocotyle illensis* (Ziegler, 1883) [=*R. campanula* (Dujardin, 1845)], have been recognized. The nomenclatural history of these species is complex and confused because the names were based upon larval forms, although the nomenclature at the adult forms are relatively clear. The name *B. polymorphus* was based on the cercaria, but it has been shown that these develop into adult trematodes called *Rhipidocotyle campanula* (Dujardin, 1845), a senior synonym of *R. illensis* (Ziegler, 1883). An extensive correspondence has taken place on this matter and it is still waiting for a decision of the International Comission on Zoological Nomenclature (see Baturo, 1979; 1992).

In the course of examining fish parasites in relation to industrial pollution (Valtonen & Koskivaara, 1989) bucephalid metacercariae were encountered in roach (*Rutilus rutilus*) from three lakes in central Finland. Since the identification of bucephalid metacercariae is not possible but is based on larval and adult stages, large scaled studies on Finnish bucephalid life-cycles were needed. Unionid bivalves were known to serve as the first intermediate hosts (e.g. Baturo, 1977; Chernogorenko, 1983) and predatory fish such as pike (*Esox lucius*) or zander (*Stizostedion lucioperca*) (e.g. Kozicka, 1959) as final hosts in European freshwaters. Lake Saravesi in central Finland was chosen as the study area due to the high prevalence of metacercariae found in roach (Valtonen & Koskivaara, 1989). Two types of bucephalid cercariae were found in *Anodonta anatina* and experimental studies on their life cycles in the laboratory were needed. This was the only way to connect the results of field studies and the life cycle stages,

and experimental studies also provided material for solving questions concerning the taxonomy of bucephalids in the area.

The process lead to the description of a new *Rhipidocotyle* species, *R. fennica* Gibson, Taskinen & Valtonen, 1992. This species was a common parasite of *A. anatina* from Lake Saravesi, while another *Rhipidocotyle* species found in the lake, *R. campanula* (Dujardin, 1845), was rare. For this reason a study was also conducted in Lake Kuivasjärvi in Oulu, northern Finland. This lake was known to have a dense population of *A. anatina* (Jokela *et al*. 1991) which were found to be infected only with *Rhipidocotyle campanula*.

After solving the taxonomical problems of Finnish bucephalids in *Anodonta anatina*, more detailed studies on the clam-parasite relationships were performed. At that stage the aim was to examine basic features of the biology of the cercariae. Furthermore, the seasonal aspects of bucephalid infections, the distribution of parasites in molluscan hosts and the distribution of *R. fennica* in the host population, as well as the significance of *R. fennica* to the reproduction of *A. anatina* were studied. An attempt was also made to view the host-parasite relationship from an evolutionary standpoint.

2. Study areas

The study was conducted in two lakes: Lake Saravesi in central Finland ($62^{\circ}25'$N, $26^{\circ}00'$E) and Lake Kuivasjärvi in northern Finland ($65^{\circ}00'$N, $25^{\circ}30'$E) (Fig. 3 in **I** and Fig. 1 in **III**).

Lake Saravesi is part of the Kymijoki water system which flows into the Gulf of Finland, Baltic Sea. It is a small (7.8 km²), shallow (mean depth 5.5 m), eutrophic, river-like lake which contains traces of organic chlorinated compounds from the effluent of paper and pulp mills 25 km upstream. It is ice-covered on average from late November until early May and highest water temperatures ($20\text{-}24^{\circ}$C) are reached at the end of July or early August. At least 14 fish species inhabit the lake, the commonest being roach, perch and pike, with zander reintroduced in mid 1980's. The clams were collected from a bay of the lake; from the littoral zone (emergent and floating macrophytes, depth < 2 m) and from the sublittoral zone (submerged macrophytes, depth 2-4 m). The bottom consists of clay with a 5-20 cm layer of organic material.

Lake Kuivasjärvi is a very small (0.84 km²), shallow (mean depth 1.9 m), hypereutrophic lake which is covered by ice from late October

until early May. Maximum water temperatures (20°C) occur in July. It flows into the Bothnian Bay, Baltic Sea. The narrow littoral zone of the lake consists of sand and has a dense *A. anatina* population. At least five fish species occur in the lake, of which roach, perch and pike are the most common. The zander does not inhabit this lake.

3. Material and methods

Only the basic information is given here, the detailed material and methods utilized in this study are described in the section "Material and methods" in articles **I-V**.

3.1. Sampling and examination of the clams

The clams were collected using a bottom dredge of mesh size 15 mm and 20 mm in Lake Saravesi and Lake Kuivasjärvi, respectively. Forty-three samples of about 30 clams each were taken from the littoral and sublittoral zones of Lake Saravesi (Fig. 1 in **II**) between May 1987 and November 1989, totalling 1,157 *A. anatina*, 29 *Pseudanodonta tumidus* Rossmässler and 65 *Unio* spp. (*U. tumidus* Philipsson and *U. pictorum* (L.)). This material was used in articles **I, III, IV** and **V**. Thirty-one samples of about 50 clams were taken from three areas of the littoral zone of Lake Kuivasjärvi (Fig. 1 in **III**) between April and October 1989 totalling 1,486 *A. anatina*. This material was used in **III** and **IV**. A sample of 168 *A. anatina* was also collected from the littoral zone of Lake Kuivasjärvi in June 1988, this material being used in **I**.

The tissues of the clams were pressed piece by piece between two large glass plates and examined using transmitted light and 12-25 x magnification. The numbers of sporocysts (the intensity of infection), the proportion of old, empty sporocysts, and the proportion of different developmental stages of cercariae were estimated from the gonads (**III, IV, V**).

The sex of clams was determined from the gonads using the presence of egg cells as the criterion for a female (**III, V**). The age was determined from rings on the shell (Crowley, 1957; Haukioja & Hakala,

1978b) (III, IV, V) and length was measured to the nearest millimeter (V). The occurrence of glochidia-larvae was estimated visually from the outer gill blade from the right side of the molluscs (III, V) and the number of egg cells in the gonads was also estimated (V).

3.2. Life-cycle studies

Life-cycles of the bucephalids were followed in the laboratory. *Anodonta anatina* shedding cercariae of either *R. fennica* or *R. campanula* were put in aquarium together with uninfected roach, which were from Lake Peurunka where unionid bivalves (and bucephalid parasites) do not occur (Valtonen & Koskivaara, 1989). The roach were thereafter fed *ad libidum* to uninfected pike, or uninfected perch were force-fed with pieces of the roach. In addition, roach collected from the lakes were fed to uninfected pike and to uninfected perch. Pike and perch used in these experiments were also from Lake Peurunka. Altogether, 76 perch and 7 pike were experimentally infected and studied during 1988-89. In addition, 155 perch, 15 pike-perch, 26 pike and 3 burbot (*Lota lota* L.) from Lake Saravesi and 163 perch and 31 pike from Lake Kuivasjärvi were examined for adult bucephalid digeneans in intestine. For the metacercarial stage, 90 roach from Lake Saravesi and 12 roach from Lake Kuivasjärvi were studied (I, II).

     Adult bucephalids were fixed in glacial acetic acid, stored in 70-80 % alcohol, stained in Mayer's paracarmine and mounted in Canada balsam, and 20 morphological features (variables 1.-20. II p. 2) were measured for species discrimination (II).

3.3. Statistical analyses

The material of this study formed mainly frequency data, which were analysed using X^2-tests (III, IV, V) loglinear models (V) and logit models (V). The t-test was used in analysing the difference between the parasite species in the development rate of cercariae (I) and adult worms from pike, perch and zander were discriminated using principal component analysis (PCA) (II).

4. Results

4.1. *Anodonta anatina* of Lake Saravesi and Lake Kuivasjärvi

The age of *A. anatina* collected from the littoral zone of Lake Saravesi ranged from 1+ to 15+ years and from the sublittoral zone from 1+ to 14+ years. The commonest age group in the material from the littoral zone of Lake Saravesi was 4 years and in the sublittoral area 6 years. The age distributions of clams from these two habitats differed from each other, more young being present in the littoral zone. Lengths of *A. anatina* ranged from 11 mm to 112 mm in the littoral zone of Lake Saravesi and from 20 mm to 97 mm in the sublittoral area, the most frequent size class being 70-79 mm in both habitats. Age-specific lengths of *A. anatina* were found to be bigger in the littoral zone of Lake Saravesi when compared to the sublittoral zone, which indicates a faster growth rate of the clams in the former habitat (**V**).

Some female *A. anatina* specimens from the littoral zone of Lake Saravesi were gravid at 2 years of age but all females could be considered to be mature at the age of 4 years in that habitat. *A. anatina* from the sublittoral zone started glochidia production one year later than in the littoral zone (**V**).

In Lake Kuivasjärvi the glochidia disappeared from the gill blades of *A. anatina* suddenly during late May and new glochidia developed during July in 1989. In Lake Saravesi the disappearance of glochidia continued until June and new glochidia developed during August in 1987-89.

The sex-ratios (females: males) of uninfected *A. anatina* from the littoral (n=287) and sublittoral (n=96) zones of Lake Saravesi were 1.12:1 and 1:1, respectively.

4.2. Bucephalid digeneans of unionid bivalves from Lake Saravesi and Lake Kuivasjärvi and the parasite life-cycles

Of the 1,157 *Anodonta anatina*, 29 *Pseudanodonta complanata* and 65 *Unio* spp. (*U. tumidus* and *U. pictorum*) from lake Saravesi, 33.2 % of *A. anatina* were infected with a bucephalid digenean which produced cercariae with long, filamentous furcae (Type A, Fig. 1 in **I**) that resembled those

described by Baturo (1977) under the name *Bucephalus polymorphus* von Baer, 1827. One percent of *A. anatina* were infected with bucephalid digenean which produced cercariae with short stout furcae (Type B, Fig. 2 in I) which resembled those described by Baturo under the name of *Rhipidocotyle illense* (Ziegler, 1883) [now *R. campanula* (Dujardin, 1845)]. Other unionids were not parasitised but parthenitae of *Phyllodistomum* sp. were also found in two *A. anatina* specimens. Of the 1,486 *A. anatina* from Lake Kuivasjärvi, only bucephalid Type B was found in 4.7 % of the clams.

Although bucephalid Type A cercaria resembled *B. polymorphus* in gross morphology, only adults of the genus *Rhipidocotyle* Diesing, 1858, were found in pike, perch and zander from Lake Saravesi. Experimental life-cycle studies confirmed this observation. Type A developed and became gravid only in pike and Type B only in perch (I).

Type B was indentified as *R. campanula*. Its first intermediate host is *Anodonta anatina*, the second intermediate host is roach and the main final host is perch, although it occurred also in zander. Type A was a new species to science and was described in article II under the name *Rhipidocotyle fennica*. Its first intermediate host is *A. anatina*, the second intermediate host is roach and the main definitive host is pike.

4.3. Ecology of *Rhipidocotyle fennica* and *Rhipidocotyle campanula*

4.3.1. Sporocyst stage

R. fennica occurred more frequently in the littoral zone (40.4 %) of Lake Saravesi than in the sublittoral area (18.1 %). *R. campanula* and its intermediate host *A. anatina* was found only from the littoral zone of Lake Kuivasjärvi, the prevalences being similar in the three sampling sites (III). No seasonality in the prevalence of infection was found in either of the parasite species (III). The sporocysts of *R. fennica* and *R. campanula* were tubular and branched. The most favoured site of the sporocysts was the gonad which was occupied in 92 % and 100 % of the clams infected with *R. fennica* and *R. campanula*, respectively. The sporocysts were also frequently found in the kidney and mantle, but less commonly in the digestive diverticula and gills, and very rarely in the foot. The prevalence of *R. campanula* infection was higher in the gonad and kidney when compared to *R. fennica*. However, in the mantle, digestive diverticula and foot the prevalence of *R. fennica* was higher. The proportion of infected

clams in which the gonad was heavily parasitised was 90 % for *R. campanula* and 30 % for *R. fennica*, and the proportion increased with host age for both species. Low intensities of infection were observed most frequently in the spring. Old, empty sporocysts of *R. fennica* first appeared in the clams during August after the beginning of cercarial emergence, and disappeared slowly thereafter. In *R. campanula* the occurrence of old sporocysts was not so obviously linked with cercarial emergence (**IV**).

Only the mature *A. anatina*, ≥ 3 and ≥ 4 years in the littoral and sublittoral zones of Lake Saravesi, respectively, were infected with *R. fennica*. The prevalence of *R. fennica* increased linearly with size of the clams; the age-prevalence curve increased among young clams but decreased among old ones. In the littoral zone of Lake Saravesi the prevalence of *R. fennica* in *A. anatina* older than 8 years was lower than could be predicted from the length of the clams. The results indicated that fast growing clams have a higher risk of becoming infected with *R. fennica* than the slow growing ones (**V**).

4.3.2. Cercarial stage

The emergence of *R. fennica* cercariae in Lake Saravesi began during July and continued throughout September, while that of *R. campanula* in Lake Kuivasjärvi occurred from Mid-June to Mid-August. The sum of day-degrees, calculated from the 1 st of May to the day of the beginning of cercarial emergence, was 1030 in 1987 and the water temperature at that date was 19.0°C. The same figures for *R. campanula* from Lake Kuivasjärvi in 1989 were 515 and 16.8°C, respectively (**III**). Under laboratory conditions the intra-molluscan development of *R. campanula* in increasing temperature, indicated by the emergence of the first cercariae, was also faster than that of *R. campanula*. In addition, both species were able to shed cercariae outside the natural emergence period when the water temperature was increased (**I**). The shedding of *R. fennica* cercariae was intermittent and lasted up to 72 days in the laboratory (**III**).

Four developmental stages of cercariae were distinguished (Fig. 3 in **IV**). Mature cercarine were found in the sporocysts of *R. fennica* in detectable numbers only during the period of cercarial emergence, but in *R. campanula* they were also found quite abundantly outside that period (**IV**).

During a 24 hour period *A. anatina* from Lake Saravesi shed on average 9,500 *R. fennica* cercariae in the laboratory, whereas the average number of *R. campanula* cercariae emerging from *A. anatina* from Lake Kuivasjärvi was only 1,400. Whilst the vast majority of *R. fennica* cercariae

were shed during the morning, this was the period of lowest emergence for *R. campanula* (I). The cercariae of *Rhipidicotyle campanula* lived longer than those of *R. fennica* (I).

The cercariae of *R. fennica* were found to select skin and fins, especially the tail of roach, as their encystment site in experimental infections. In contrast, cercariae of *R. campanula* encysted almost without exception in the gills of roach (I).

The chaetotaxy of *R. fennica* cercariae was described in article II.

4.3.3. Metacercarial and adult stages

In experimental studies, cercariae of *R. fennica* encysted mainly in the skin and fins of Lake Saravesi roach. In Lake Kuivasjärvi, where only *R. campanula* occurs, metacercariae were mainly found in the gills of roach (I). In addition, in Lake Saravesi the prevalence and intensity of bucephalid infection were highest in pike (46.1 %, mean intensity=105 worms/fish, n=26). The same figures for zander and perch were 13.3 %, 30 worms/fish, n=15 and 11.0 %, 5.3 worms/fish, n=155, respectively. Mature worms were found from all three host species. In Lake Kuivasjärvi the prevalence of infection was higher in perch (20.9 %, n=163) when compared to pike (12.9 %, n=31), and mature specimens were found only in perch (I). The results of experimental infections of final hosts were consistent with field observations. The prevalence and intensity of infection with *R. fennica* in pike were higher (n=5, 100 %, x=210 worms/fish) than in perch (n=53, 12.5 %, x=2.3 worms/fish), and mature worms were found only in pike. The prevalence and intensity of infection with *R. campanula* were higher in perch (n=20, 68.2 %, x=19.4 worms/fish) than in pike (n=2, neither was infected), and mature worms were found only in perch.

The best morphological feature to distinguish the metacercariae of *R. fennica* and *R. campanula* was the position of the pharynx along the body, which is more posterior in *R. fennica* than in *R. campanula*. Adult *R. fennica* can be distinguished from *R. campanula* by its smaller egg-size, more posterior position of the pharynx, more anterior position of the ovary and anterior testis in relation to the pharynx, and more posterior position of the anterior margin of the vitelline fields (II).

Adult *R. fennica* in Lake Saravesi and *R. campanula* in Lake Kuivasjärvi were gravid in late summer and autumn. Thus, the miracidia of these parasites are only present in the lakes at that particular time (I).

4.4. Effect of *Rhipidocotyle fennica* on the reproduction of *Anodonta anatina*

The egg cell production of *A. anatina* decreased with the increasing intensity of *R. fennica* infection in the gonads of host. The infection also decreased the glochidia production of *A. anatina*. In mature clams (≥ 4 years) 55.4 % and 44.4 % of the uninfected molluscs carried glochidia in the littoral and sublittoral zone of Lake Saravesi, respectively, while among infected clams the figures were 18.5 % and 18.8 %. It could be estimated that one third of female *A. anatina* from the littoral zone of Lake Saravesi were not able to reproduce because of an *R. fennica* infection (**V**).

5. Discussion

5.1. Distribution *Rhipidocotyle fennica* in *Anodonta anatina* population of Lake Saravesi

The absence of infections in immature clams can be explained in several ways. Perhaps the entry of *R. fennica* miracidia into young *A. anatina* or their further development is not successful. During maturation the epithelium of *A. anatina* may change, making the penetration of miracidia possible, or the structure (e.g. space) or chemical composition (e.g. energy) of clam tissues may change allowing the growth of parasite sporocysts. The immunological responses of *A. anatina* against *R. fennica* may also disappear accompanied with maturation. In mature *A. anatina* only insignificant attempts to prevent the sporocysts from spreading throughout the host have been observed (Haaparanta & Valtonen, unpubl.). The resistance of molluscs against trematodes can be highly costly, for example energetically (Minchella, 1985). However, the costs of being infected, measured as a total life-time reproductive output, can be expected to be very high in juvenile *A. anatina* but lower in adult, mature, already reproduced clams. Instead of that, the costs of resistance can be expected to be high in adults in which the resources allocated to perhaps highly energy-demanding resistance can decrease those available for reproduction, comparing to juveniles, which do not reproduce. Under

these circumstances the juvenile clams would be survival-selected and the adults reproduction-selected, if the prevalence of infection is high. Thus, an immunity which disappears during maturation could have been evolved. It is also possible that miracidia of *R. fennica* do not find immature *A. anatina*, which are totally burrowed into the sediment whereas the mature clams are epibenthic (burrowing depth of *A. anatina* observed by J. Jokela in laboratory and field).

The filtration rate of *A. anatina* increases with the size of the clam (Kryger & Riisgård, 1988). Although this cannot explain the absence of infections in young clams, it may contribute to the increasing prevalence with the size of the clams bigger than 50 mm in length. The advantages for *R. fennica* to select big hosts are obvious (abundance of space, energy and nutrients), but what is the mechanism by which a miracidium can asses the size of a clam? The height of the siphons above the bottom surface, the siphon-sediment-distance (SSD), could serve as a reliable cue for the size of a clam. Perhaps the miracidia of *R. fennica* locate the clams by a chemotactic response, avoid the vicinity of the bottom surface because of a risk of entanglement in the sediment and leave endobenthic clams unattacked, are carried into big clams due to strong inhalant water current or they also may actively choose big clams utilizing the SSD, for example (**V**).

The bigger size of infected molluscs is often interpreted as a consequence of trematode-induced growth acceleration due to parasitic castration which causes most of the reproductive energy to redicte to somatic growth (see e.g. Minchella, 1985). However, the results of this study indicate that rapid growing *A. anatina* have a higher risk to get infected by *R. fennica* (**V**). This enables a potential of *R. fennica* to influence on the life-history evolution of *A. anatina*. Growth rate is an essential life-history parameter of *A. anatina*; according to Haukioja & Hakala (1978a), a rapid growth of *A. anatina* occur together with a high clutch size, high reproductive effort and a short reproductive life-span.

The higher prevalence of *R. fennica* in the littoral zone of Lake Saravesi may be a consequence of a higher density of pike, the final host of the parasite, in that habitat when compared to the sublittoral area (**I**). In addition, according to the "SSD-hypothesis", the bigger age-specific sizes of *A. anatina* in the littoral zone and harder sediment may also contribute to the more frequent parasitisation rate of the clams.

The higher prevalence of infection among female clams may again be, connected with bigger size of the female clams, although such factors as easier penetration, metamorphosis or growth of *R. fennica* in females, higher parasite-induced mortality in males or sex-change due to infection can also be involved (**V**).

5.2. Distribution of *Rhipidocotyle* species in *Anodonta anatina* individual and timing of cercarial production

By definition, a parasite is harmful to its host (Price, 1980): the extreme effect is that it kills the host. Bucephalid digeneans, according to Lauckner (1983), cause the death of the host clam sooner or later. In their resource allocation hypothesis, Williams (1966a) and Charnov & Krebs (1973) assumed that reproduction decreases the probability of survival. The reproductive activities of bucephalids decrease the probability of the survival of their host clams and, consequently, themselves. Thus, the increased risk of death can be considered as a cost of reproduction in bucephalid digeneans. It can be assumed that the more a bucephalid digenean produces cercariae the higher is the probability that the host will die. Other factors of bucephalid reproduction, which presumably affect the survival of the host, include e.g. (1) in which organs of the clam the sporocysts are located, (2) which substances are used as a source of energy, and (3) the timing of cercarial production. Through the survival of the host, these factors all affect the number of future reproductive seasons of the parasites. Natural selection should maximize the total life-time reproductive output (R) of a bucephalid in a clam, which is a product of the number of reproductive seasons (N_{RS}) and the number of cercariae produced per reproductive season (N_C/rs); i.e. $R = (N_C/rs) \times (N_{RS})$. To maximize that product, the selection should optimize the N_C/rs-N_{RS}-ratio since, as discussed above, an increase in the N_C/rs should result in a decrease in the N_{RS}. The main factors which affect the N_{RS} of a bucephalid in a clam are the expected natural life span of the host and the effects of the parasite on the host body. Two predictions can be made in this situation. Firstly, under circumstances in which the expected N_{RS} is low or unpredictable, selection should favour a high N_C/rs of a parasite. Secondly, the higher and more predictable the expected N_{RS}, the more important the N_{RS} becomes to the total reproductive output of a parasite, and, consequently, a higher fitness response might be expected to result from all of the adaptations of the parasite which improve the survival of the host.

Since *A. anatina* is a long-lived clam, the residual reproductive value (Williams, 1966b) of a parasite individual is generally high as long as it does not kill the host quickly. According to Haukioja & Hakala (1978) and Tuomi, Hakala & Haukioja (1983), the reproductive effort of *A. anatina* is low, and so its reproduction should not significantly increase adult mortality. For this reason, the production of cercariae during the period when the host is producing glochidia, or is prepared to do so, would probably result in a lower risk of death to the host, as compared to a situation where the parasite utilised the same amount of energy at some other period. At that time the energy utilised by a parasite might be

expected to reduce the resources which have allocated for the reproduction of the host rather than those used for its general maintenance. It is worth noting that (1) most preferred site of infection for *Rhipidocotyle* spp. is the gonad, (2) the gonadal tissue is partly or completely replaced by *Rhipidocotyle* spp. sporocysts in the infected clams, and (3) the production of glochidia is highly reduced or non-existant in infected clams. The difference in the timing of cercarial emergence between *R. fennica* in Lake Saravesi and *R. campanula* in Lake Kuivasjärvi, and their close concurrence with the development of the host's glochidia in both lakes, might indicate that *Rhipidocotyle* spp. are able to synchronise their reproduction with that of the host. By behaving in this way, they might be expected to obtain as much energy and nutrients as possible with minimum negative effects on the survival of the host. Futhermore, it can be assumed that the infected clams are prepared for reproduction and their food intake is at its highest level at this time, even though their gonads are full of bucephalid sporocysts.

The destruction of the reproductive organ of the mollusc may be expected to be less critical for the survival of the host when compared, for example, to the gills, kidney area or digestive diverticula, which may explain the invasion of the gonad. By invading the gonad instead of some other "important" organ(s) the trematodes can keep the host alive and, therefore, survive themselves for a longer period. In the present lakes, *A. anatina* can live over 15 years. In such a long-lived host this kind of behaviour of the parasite (a sparing tactic) could be adaptive, because the expected life span of both the host and the parasite is long and the residual reproductive value (RRV) (Williams, 1966) of the parasite is high if the parasite acts in a way that the host does not die quickly. However, the long survival of the host is not necessarily the only possible strategy for the parasite to obtain an advantage from the host. A quick and massive removal of energy and nutrients kills the host sooner, but benefits the parasite through a greater cercarial production per unit of time. In addition, provided that the host survives long enough for the parasite to complete its development and that the host population can survive, it may not be important for the parasite if the impact on the individual host was severe. As soon as the armada of cercariae has been released into the environment, the molluscan host individual is no longer needed, as has been stated by Wright (1971) and Lauckner (1986). This kind of behaviour of the parasite (an exhaustion tactic) may be predicted to be adaptive in short-lived molluscan hosts, where the expected life span of the host is short even without the parasite, and, for this reason, the RRV of the parasite is low. In molluscs which have a short life span, a greater total output of cercariae during the mollusc life-time may be achieved by the parasite when using the exhaustion tactic rather than the sparing tactic. In molluscs with a long life span, such as *A. anatina*, the situation could be predicted to be the reverse.

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5.3. Pathogenity of *Rhipidocotyle* species

The organs of *A. anatina* can be ranked into two classes according to their importance to the mollusc. There are organs such as the gills, digestive diverticula and kidney region, including the heart, which are important for the vital functions of the mussels. Damage in organs such as the gonad and mantle can be assumed to be less harmful over a limited period of time. The pathogenicity of a digenean parasite is at least partly determined by its location and by the amount of sporocysts. When assessing the relative pathogenicity of *Rhipidocotyle* species in this study, the infection in the "important" organs is the determining factor. In both species the numbers of sporocysts were very low in the digestive diverticula but frequently high in the region of the kidney. Thus the prevalence of infection in the region of the kidney could be regarded to be a critical parameter determining the expected pathogenicity. The proportion of infected clams harbouring *R. campanula* sporocysts in the kidney region was remarkably higher when compared to *R. fennica* infected clams, and *R. campanula* might, therefore, be expected to be more pathogenic than *R. fennica* to *A. anatina*. Because no prominent immunological response of *A. anatina* against *R. fennica* has been found (Haaparanta, A. & Valtonen, E. T., unpubl.), the considerably higher proportion of clams heavily infected by *R. campanula*, and the faster development of its weak infections into heavy infections during the summer, indicates that a *R. campanula* infection reaches its terminal stage much more quickly in *A. anatina* than *R. fennica*.

The proposed higher pathogenity of *R. campanula* in *A. anatina* may result as a higher parasite-induced mortality of the host as compared with *R. fennica*. This might contribute to the lower *R. campanula* prevalences in both study lakes when compared to the prevalence of *R. fennica* infection in Lake Saravesi.

6. Conclusions

Because many studies on bucephalid digenean have only minimal scientific value due to the confused nomenclature, (1) experimental life-cycle examinations or (2) detailed morphological descriptions of the bucephalid parasites, no matter if they were studied in sporocyst, cercarial, metacercarial or adult stage, are needed.

Both *Rhipidocotyle* species frequently filled the gonad and, in

advanced infections spread through almost all tissues of the clam. This and other potential consequences of *Rhipidocotyle* infections should be taken into account when *A. anatina* individuals, populations or communities which they participate, are studied. For example, the effect of *Rhipidocotyle* infections on the accumulation rate of e.g. organochlorine compounds into tissues of *Anodonta anatina* ought to be examined.

When bucephalid digeneans in *Anodonta anatina* are studied the seasonal dynamics in the development and emergence of cercariae and in the development of sporocysts, as well as the dependence of the prevalence and intensity of infection on the age of the host, and the relationship between the prevalence of infection and habitat, sex and size of the host should be taken into account.

Acknowledgements

Yhteenveto

Rhipidocotyle-imumatojen ekologiasta Laukaan Saravedessä ja Oulun Kuivasjärvessä.

Väitöskirjassani olen tutkinut kahden *Rhipidocotyle*-suvun imumatolajin ekologiaa elämänkierron eri vaiheissa Laukaan Saravedessä Keski-Suomessa ja Oulun Kuivasjärvessä vuosina 1987-89. Työssä tutkittiin yhteensä 2,737 suursimpukkaa ja 506 luonnonkalaa. Lisäksi kuudessa laboratoriokokeessa tai -seurannassa, jotka yleensä koostuivat monista erillisistä koejaksoista, käytettiin tai tutkittiin yhteensä 563 kalaa ja 608 pikkujärvisimpukkaa.

  Rhipidocotyle-imumadot kuuluvat pääjaksossa laakamadot (Platyhelminthes) luokkaan imumadot (Digenea) ja heimoon Bucephalidae. Kyseisen heimon lajien elämänkierto on monimutkainen sisältäen kaksi vapaana ja kolme loisena elävää vaihetta. Bucephalidien ensimmäisen väli-isännän, simpukan, sisällä elävää vaihetta kutsutaan sprokystiksi, joka tuottaa suvuttomasti kerkaria-toukkia. Ne poistuvat simpukasta, tarttuvat ja tunkeutuvat särkikaloihin (toinen väli-isäntä) muuttuen metakerkarioiksi. Kun petokala (pääisäntä) syö loisitun särkikalan, loiset kehittyvät aikuisiksi petokalan suolessa ja tuottavat munia, joista vedessä kuoriutuu mirakidium-toukkia, mitkä etsiytyvät jälleen simpukkaan aloittaen elämänkierron alusta.

  Työ tehtiin Jyväskylän yliopiston biologian laitoksella ja se koostui kahdesta osasta: (1) imumatojen elämänkierron ja lajiston kuvaus ja (2) niiden ekologian selvittäminen elämänkierron eri vaiheissa, etenkin pikkujärvisimpukassa. Äänekosken puunjalostustehtaiden alapuolella sijaitsevan Saraveden särjissä havaittiin voimakas Bucephalidae-loisinta. Järven hauista ja ahvenista löytyi *Rhipidocotyle*-suvun imumatoja. Kirjallisuuden mukaan Euroopan sisävesissä esiintyy kaksi tämän heimon edustajaa, lajit *Rhipidocotyle campanula* ja *Bucephalus polymorphus*. Pikkujärvisimpukoista löydettiin kahta *Bucephalidae*-lajia, joista toinen kuului *Rhipidocotyle*-sukuun, mutta toinen vaikutti kuuluvan sukuun *Bucephalus*. Muissa suursimpukkalajeissa imumatoja ei esiintynyt. Koska Saraveden kaloista oli löydetty vain sukua *Rhipidocotyle*, jouduttiin loisten elämänkierrot selvittämään laboratoriossa. Simpukoista tulleita, tietyn tyyppisiä kerkaria-toukkia tartutettiin loisettomiin särkiin. Särjet syötettiin loisettomille hauille ja ahvenille. Niiden ruuansulatuskanavassa aikuistuneista madoista havaittiin, että Saravedessä esiintyi kaksi *Rhipidocotyle*-imumatolajia; *R. campanula* ja tieteelle uusi laji, jolle annettiin nimeksi *Rhipidocotyle fennica*. *R. fennica*n pääisäntä oli hauki ja *R. campanula*n ahven. Molempien lajien ensimmäisenä väli-isäntänä oli pikkujärvisimpukka (*Anodonta anatina*) ja toisena väli-isäntänä särki. Särjessä *R. fennica* hakeutui eville ja iholle, *R. campanula* kiduksille.

  Saraveden pikkujärvisimpukoista 33.2 %:lta löytyi *R. fennica*a ja 1.0 %:lta *R. campanula*a. *R. fennica* oli yleisempi rantavyöhykkeessä kuin ulapalla. Naarassimpukat, suurikokoiset, iäkkäät ja nopeakasvuiset

simpukat olivat useammin loisittuja kuin koirassimpukat, pienet, nuoret tai hidaskasvuiset simpukat. Loiset tuhosivat usein simpukan sukurauhaset. Saraveden rantavyöhykkeen pikkujärvisimpukkanaaraista voitiinkin arvioida joka kolmannen olleen kykenemätön lisääntymään *R. fennica*-infektion vuoksi.

Tutkimus laajennettiin myös Oulun Kuivasjärvelle, jossa tiedettiin olevan tiheä simpukkakanta. Tämän järven pikkujärvisimpukoista 4.7 %:lta löytyi *R. campanula*-imumatoa, mutta *R. fennica* puuttui. Loisittujen simpukoiden osuudessa ei esiintynyt vuodenaikaisvaihtelua kummallakaan lajilla kummassakaan järvessä. Saravedessä *R. fennican* kerkaria-toukkia tuli ulos simpukoista heinäkuulta syyskuulle, mutta *R. campanula*t "parveilivat" Kuivasjärvessä aikaisemmin, kesäkuun puolivälistä elokuun puoliväliin. Molemmissa järvissä kerkariat parveilivat kuitenkin pikkujärvisimpukan lisääntymisaikaan. Jälkeläismääränsä lisäämiseksi loiset ehkä ajoittavat oman lisääntymisensä simpukan lisääntymisjaksoon, koska tällöin simpukoiden ravinnonotto ja energiavarat ovat suurimmillaan. Pisin laboratoriossa mitattu *R. fennica* parveilujakso oli 72 vuorokautta, mutta parveilussa saattoi esiintyä useankin vuorokauden katkoja. Simpukkaa kohden *R. fennica* tuotti keskimäärin 9 500 kerkaria-toukkaa vuorokaudessa, pääasiassa aamulla ja päiväsaikaan, mutta vastaava *R. campanula*n vuorokautinen kerkariatuotanto oli vain 1 400 ja tapahtui lähes pelkästään yöllä. *R. fennica*n kerkarioiden elinikä oli kuitenkin lyhyempi (keskimäärin 17 tuntia) kuin *R. campanula*n (keskimäärin 28 tuntia).

Molemmat lajit valitsivat useimmiten simpukoiden sukurauhaset olinpaikakseen jättäen elintärkeät elimet rauhaan. Näin loiset todennäköisesti vähentävät vahingollista vaikutustaan isäntäänsä kohtaan, jolloin myös niiden oma elinikä pitenee. *R. campanula*n infektoimissa pikkujärvisimpukoissa sporokystien määrä oli suurempi kuin *R. fennica*lla. Ilmeisesti *R. campanula*n vahingollisuus pikkujärvisimpukkaa kohtaan on suurempi kuin *R. fennica*n. *R. campanula*n loisimien simpukoiden nopeampi kuolema voisikin osaltaan selittää sen alhaisempaa esiintymistä Saravedessä ja Kuivasjärvessä *R. fennica*an verrattuna.

Koska *Rhipidocotyle*-imumadot näyttävät olevan yleisiä loisia ja niillä on voimakas vaikutus simpukan elintoimintoihin, ne olisi otettava aina huomioon tutkittaessa pikkujärvisimpukkaa, simpukkayksilöä tai populaatiota sekä eliöyhteisöä, jossa simpukka on mukana, erityisesti myös silloin kun simpukoita käytetään ympäristömyrkkyjen seurantaan.

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ORIGINAL PAPERS

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II

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III

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IV

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V

AGE-, SIZE- AND SEX-SPECIFIC INFECTION OF
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