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Author's address   Katja Pulkkinen
Department of Biological and Environmental Science
University of Jyväskylä,
P.O. Box 35,
FIN-40351 Jyväskylä, Finland

E-mail: pukaan@cc.jyu.fi

Supervisors   Professor E. Tellervo Valtonen
Department of Biological and Environmental Science
University of Jyväskylä,
P.O. Box 35,
FIN-40351 Jyväskylä, Finland

Docent Ilppo Vuorinen
Archipelago Research Institute
University of Turku,
FIN-20500 Turku 50, Finland

Reviewers   Professor Karin Andersen
Zoological Museum
University of Oslo,
Sarsgatan 1,
N-0562 Oslo 5, Norway

Professor Kenneth MacKenzie
Department of Zoology
University of Aberdeen,
Tillydrone Avenue,
Aberdeen AB24 2TZ, United Kingdom

Opponent   Professor Clive Kennedy
Department of Biological Sciences
University of Exeter,
Exeter EX4 4PS, United Kingdom

ABSTRACT

Factors affecting transmission of *Triaenophorus crassus* (Cestoda) from copepod first to coregonid second intermediate hosts were studied using field data from three areas at Lake Saimaa, SE Finland, as well as data from experimental infections of hosts in the laboratory. In Lake Saimaa whitefish (*Coregonus lavaretus* s.l.) were frequently infected with *T. crassus* plerocercoids, but vendace (*C. albula*) only accidentally. Stomach samples indicated that both fish species consumed copepod species that were suitable as hosts. In experimental infections whitefish became infected with *T. crassus* but vendace did not. Abundances of a benthically transmitted nematode *Cystidicola farionis* in whitefish indicated that as a superior competitor for planktonic food, vendace, when abundant, may displace whitefish from feeding on plankton and force it to rely more on benthic food. Vendace stock strength did not, however, affect the abundance of *T. crassus* in whitefish. This is possibly due to synchronization of the transmission of the parasite to the seasonal feeding behaviour of coregonids in spring in the littoral zone, when copepods are the only abundant food available for both whitefish and vendace. Vendace, however, do not become infected even though they eat infected copepods, since *T. crassus* is less infective for vendace than whitefish. In the first intermediate host (*Cyclops strenuus*), *T. crassus* infection affected the copepod's feeding, fecundity and survival and caused changes in swimming behaviour and microhabitat selection and an increased susceptibility to predation by whitefish juveniles in the laboratory. However, evidence that the behavioural alterations in copepods were caused by active manipulation adaptive to the parasite was not clear. In whitefish, the accumulation of the plerocercoids seemed to increase in the oldest hosts, in which also the effects of *T. crassus* infection on growth were concentrated. However, no evidence of parasite-induced mortality was found.

Key words: Behavioural changes; copepods; *Coregonus*; *Cyclops strenuus*; *Cystidicola farionis*; growth; host specificity; transmission; *Triaenophorus crassus*.

K. Pulkkinen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 Jyväskylä, Finland

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers, which will be referred to in the text by their Roman numerals (I-V). Some unpublished data are also presented.

I   Pulkkinen, K. & Valtonen, E. T. 1998: The use of parasites as tags to elucidate differences between whitefish populations. Archiv für Hydrobiologie, Special Issues, Advances in Limnology 50: 257-271.

II   Pulkkinen, K., Valtonen, E. T., Niemi, A. & Poikola, K.: The influence of food competition and host specificity on the circulation pattern of parasites through coregonid hosts. Manuscript (submitted).

III   Pulkkinen, K. & Valtonen, E. T. 1999: Accumulation of plerocercoids of *Triaenophorus crassus* Forel (Cestoda) in the second intermediate host *Coregonus lavaretus* and their effect on growth and mortality of the host. Journal of Fish Biology 55: 115-126.

IV   Pulkkinen, K., Pasternak, A. F., Hasu, T. & Valtonen, E. T.: Effect of *Triaenophorus crassus* (Cestoda) infection on the behavior and susceptibility to predation of the first intermediate host *Cyclops strenuus* (Copepoda). Manuscript (submitted).

V   Pasternak, A. F., Pulkkinen, K., Mikheev, V., Hasu, T. & Valtonen, E. T.: Factors affecting abundance of *Triaenophorus* infection in *Cyclops strenuus*, and parasite-induced changes in host fitness. International Journal for Parasitology (accepted).

Responsibilities of Katja Pulkkinen in the articles of this thesis

Paper I. Tellervo Valtonen planned the study. I was responsible for handling the material and the data and writing most of the article.

Paper II. The study was planned together by all authors. Asko Niemi and Kauko Poikola collected the fish material from Lake Saimaa and provided the information on the study area. I was responsible for collecting all plankton material, planning, designing, setting up and running all the experiments with copepods and fish, as well as handling the data and writing the manuscript.

Paper III. The study was planned together with Tellervo Valtonen. I handled the fish material, made the statistical analyses and wrote the article.

Paper IV. I was responsible for planning the study. I designed, set up and run all the experiments together with Tiina Hasu, except for the photobehaviour experiment which was designed, set up and run by Anna Pasternak. I handled the data and wrote the manuscript.

Paper V. I planned part of the experiments (the effect of developmental stage of the copepod on acquiring coracidia, the effect of the parasite on the egg sac production and survival of the copepods) and designed, set up and run the experiments together with Tiina Hasu. Anna Pasternak and Viktor Mikheev planned, designed and run rest of the experiments (the effect of alternative food on acquiring coracidia and the effect of parasite infection on copepod feeding). Anna Pasternak and Viktor Mikheev wrote the first draft of the manuscript which was then completed by me.

Jyväskylä May 11th, 1999

Katja Pulkkinen

1   INTRODUCTION

1.1   General introduction

For a parasite with a multi-host life cycle passing from one host to another potential host, i.e. transmission, is the crucial point in the life cycle. The transmission success is determined by the spatial and temporal overlap of the infective stages of the parasites and suitable hosts. Since reaching a suitable host is of primary importance in determining the fitness of a parasite, there should be strong selection for any adaptations in the parasite which increase its chances of reaching a suitable host (Holmes 1976). At each stage in the cycle, selection favours those individuals which best can reach, establish and develop in the next host in the cycle. In cestodes three major strategies for increasing the probability of the transmission have evolved: 1) evolution of life cycles interpolated into host biology, 2) presentation of infective stages that increase the probability of contact between host and parasite and 3) increased reproductive potential (Mackiewicz 1988).

The life cycle of *Triaenophorus crassus* Forel is that of a typical aquatic pseudophyllidean cestode (Fig. 1). An individual worm maturing in the gut of the definitive host, the pike (*Esox lucius* L.), produces up to 4 millions of eggs (Shostak & Dick 1987), which are released into water during a few days in spring. Free swimming coracidia larvae hatched from the eggs, as well as the procercoid larvae that develop in the coeloma of the copepod first intermediate hosts after ingestion of coracidia, are short-lived. The life span of a coracidium is only a few days depending on water temperature and that of a procercoid a few weeks depending on the life span of the copepod (Kuperman 1973). The egg release is synchronized to exploit the seasonal concurrent occurrence of all hosts in the littoral habitat and to ensure the transmission of the parasite via the food chain from the final host to coregonid second intermediate hosts via copepods (Miller 1952, Mackiewicz 1988). Pike enters the littoral zone in spring to spawn at the same time that coregonids migrate there to feed on seasonally

available rapidly multiplying copepods. In pike the life span of the parasite is annual, the plerocercoids accumulated through the year mature at the same time and after egg release they detach from the gut wall and are evacuated into water (Miller 1952). In coregonid second intermediate hosts the parasite lives for several years (Miller 1952, Dick & Rosen 1982) and the parasites are cumulative with host age. The second intermediate host acts therefore as a reservoir host in the life cycle, ensuring the persistence of the parasite in a habitat even if the annual cycle from the final host to coregonids fails in some years.
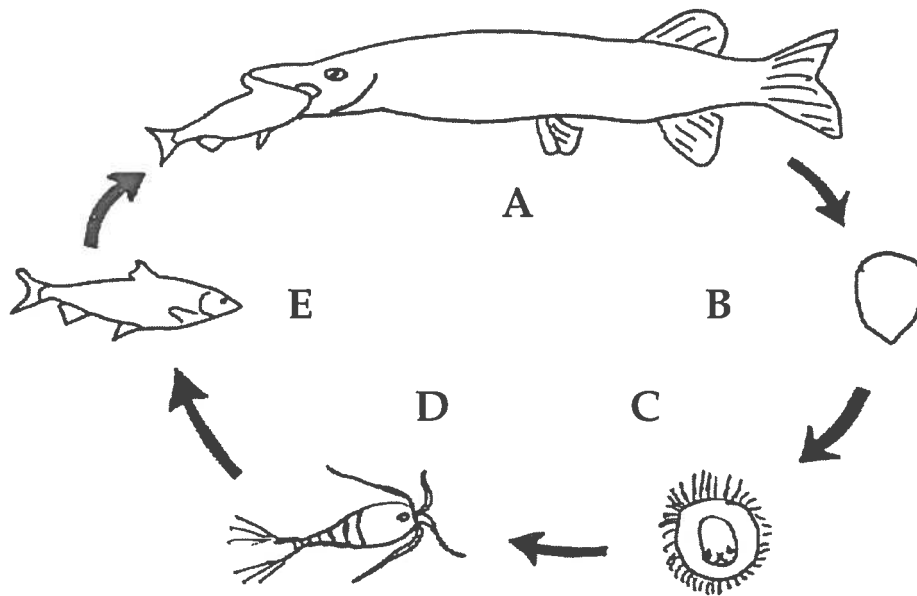
FIGURE 1   The life cycle of *Triaenophorus crassus.* A = adult worm in pike (*Esox lucius*), B = egg, C = free-swimming coracidium, D = procercoid in a copepod first intermediate host and E = plerocercoid in a coregonid second intermediate host.

The probability of a single cestode egg developing to an adult is very low (Mackiewicz 1988). High fecundity is generally considered an adaptation to counter the high mortality during transmission between hosts. Eggs and coracidia of many cestode species have morphological and behavioural adaptations that increase their probability of being eaten by the next host (Kennedy 1983, Mackiewicz 1988). *Triaenophorus* coracidia exhibit positive phototaxis, which brings them to the surface layer of the water where they are more likely to encounter copepods (Kuperman 1973). Variability in timing of the egg hatch would increase the temporal dispersion of coracidia (Shostak & Dick 1989) and spread the risk of missing the encounter with copepod hosts. However, the host finding of coracidia is passive and they do not exhibit directed behavioural responses towards copepods (MacInnis 1976, Kennedy 1983). Transmission is thus determined by environmental factors, the abundance of both parasites and hosts, and the feeding behaviour of the hosts (Mackiewicz 1988). In experiments where copepods were offered only larval

parasites to feed on, the probability of procercoid infection has been shown to increase with the increasing number of coracidia ingested (Nie & Kennedy 1993, Wedekind 1997). The resulting infection level in copepods has been found to follow a functional response curve reaching a plateau, a response typical of predator-prey interactions (e.g. Nie & Kennedy 1993, Ashworth et al. 1996). In the natural environment coracidia comprise only a small fraction of available prey items for cyclopoid copepods and the probability of coracidia being eaten may be diminished by the dilution effect and/or selective consumption. Pseudophyllidean coracidia resemble in appearance ciliate protozoans, which are preyed upon by many cyclopoids (Monakov 1976, Wickham 1995a,b). It is not known whether cyclopoids can distinguish between coracidia and ciliates and how the presence of ciliates or other alternative food items affects parasite uptake.

Incorporation of transmission into the behaviour (feeding, habitat use, migration etc.) of the hosts as such enhances the probabilities of reaching suitable hosts and decreases the probabilities of ending up in unsuitable hosts (Holmes 1976). However, in most cases predators of a particular species eat only a small proportion of a given prey species. Thus, any adaptation in a parasite which increases the chances of the infected prey animal being among those eaten by a suitable host should be strongly favoured by selection (Holmes 1976). The probability that a predator will detect a prey individual is increased once the behaviour or the appearance of the prey deviates appreciably from the norm (Mackiewicz 1988). Parasite-induced changes in intermediate host behaviour have been reported from a variety of host-parasite systems (reviews by Barnard & Behnke 1990, Beckage 1997, Hurd & Lane 1998), including various copepod-cestode systems. Both increases (Poulin et al. 1992, Urdal et al. 1995, Wedekind & Milinski 1996) and decreases (Pasternak et al. 1995) in the swimming activity and impaired escape ability (Pasternak et al. 1995, Wedekind & Milinski 1996) of infected copepods have been recorded in different copepod-cestode systems. In some cases it has been demonstrated that changes in swimming activity and escape ability make infected copepods more susceptible to predation by fish hosts (Poulin et al. 1992, Wedekind & Milinski 1996). Selection for the trait of altering host behaviour should be strongest when the resultant increase in the basic reproductive rate of the parasite and reduction in the threshold number of hosts required to sustain the parasitic infection are greatest, e.g. in cases where the distribution of the hosts is patchy and their population density is low (Dobson 1988). The critical period in the life cycle of *T. crassus* is the temporally narrow transmission window from pike to coregonids via copepods. Moreover, the prevalences of cestode procercoids in the copepod intermediate hosts including *T. crassus* are generally very low (< 2%) (Freeman 1964, Watson & Lawler 1965, Boyce 1974, Jarroll 1979, Marcogliese & Esch 1989). In coregonid hosts high burdens of *T. crassus* have been observed throughout their distribution range (Miller 1952, Petersson 1971a,b, Amundsen 1988). This indicates high transmission efficiency from copepods to coregonids. Therefore manipulation of the behaviour of the copepod host to increase its susceptibility to coregonid predation has potentially evolved in *T. crassus*.

In the life cycle of *T. crassus* the regulatory role of the abundance of the definitive host (pike) population in determining the plerocercoid abundance in the coregonid hosts has been shown in connection with intensive fishing programs (Miller 1952, Amundsen & Kristoffersen 1990). Also the effect of the density of the second intermediate host populations has been shown to affect the abundance of parasites in them, but the results of the intensive fishing programs have been less clear than in the case of the pike removals (Miller 1952). Differences in the accumulation of *T. crassus* have been found between sympatric cisco (former genus *Leucichthys*, presently *Coregonus*) forms as well as whitefish (*C. lavaretus* L. s.l.) forms differing in their morphological and behavioural characteristics (Keleher 1952, Miller 1952, Petersson 1971a,b, Amundsen 1988). In Canada, the cisco (*C. artedi* Le Sueur) has been found to be more heavily infected with *T. crassus* than the whitefish, and established as the primary second intermediate host in the life cycle of the parasite (Miller 1952). In most cases the presence of cisco in the lake has been found to be essential for the occurrence of the parasite. However, effects of composition of the host community and interactions between sympatric second intermediate hosts on the abundance of plerocercoid populations in each of the host species have not been studied, although in the case of a parasite with a multi-host life-cycle, the parasite population dynamics are likely to be affected by the structure of the host community (Holmes 1979).

The impact of parasites on the populations or distributions of their hosts is ultimately based on their impact on individual host animals (Holmes 1982). Assessing the effect of parasites on host individuals is therefore a prerequisite for studying the effect of parasites on host populations. Due to heterogeneity in exposure caused by contagious spatial and temporal dispersal of both hosts and the infective stages of parasites and differences in the behaviour of hosts, as well as to differences in susceptibility among hosts (Crofton 1971, Anderson & Gordon 1982), the frequency distributions of parasites in hosts are usually overdispersed, such that the bulk of the parasite population is aggregated in a few hosts. The effect of a macroparasite on the host is generally thought to be dependent on the number of parasites within the host (Crofton 1971, Anderson & May 1978, Anderson & Gordon 1982). In some experimental studies the impact of parasites on host survival has been shown to be directly related to worm burden (Keymer 1981, Scott & Anderson 1984). Aggregation of the parasites in few hosts means that the effects of the parasites are concentrated on a smaller proportion of the host population than in a case where the parasites are evenly distributed, which has important consequences when considering the effect of parasites on host populations.

The rate of acquisition of macroparasites can be estimated from age-prevalence or age-intensity curves in hosts that can be accurately aged (Hudson & Dobson 1995). The simplest and most commonly used measure of parasite aggregation is the ratio of the variance to the mean number of parasites per host. Ratios greater than one indicate that parasites are not distributed randomly according to the Poisson distribution, but have aggregated in a few hosts, levels of aggregation increasing with the increase in the value of the ratio. Anderson & Gordon (1982) suggested that a decline in the variance to mean

ratio together with a decrease in mean abundance in the oldest age groups of the host might be evidence of parasite-induced mortality in the oldest fish. The suggestion is based on the assumption that the effect of the parasite increases with the increase in parasite load and that the parasites live as long as their hosts or at least leave detectable marks after death (Anderson & Gordon 1982).

However, macroparasite infections are generally chronic leading to morbidity rather than mortality (Hudson & Dobson 1995). The harmful effects of the parasite on the host depend not only on the number of parasites present but also on the ecological context (Holmes 1982, Goater & Holmes 1997). The relationship between any given parasite species and an individual host can fall anywhere along a continuum from infection without discernible disease, through reduced growth and decreased condition or reproductive output of the host, to death of the host (Holmes 1982). The ability of the host to compensate for the adverse effects of the parasite is likely to vary between individuals, being lowest in hosts whose fitness has decreased due to other reasons, like malnutrition, stress or low social status (Holmes 1982, Holmes & Zohar 1990). Also the sub-lethal effects of macroparasites on host fitness have important consequences for the dynamics of the interaction between the host and parasite populations (Hudson & Dobson 1995). Reduced growth of fish hosts due to cestode infections have been attributed to *Eubothrium* sp. and *Diphyllobothrium dendriticum* infections in salmonids (Smith 1973, Bristow & Berland 1991, Rahkonen 1998). Also *T. crassus* infections have been shown to impair whitefish growth (Miller 1945) and to cause serious musculature damage to experimentally infected whitefish (Dick & Rosen 1982, Rosen & Dick 1984).

1.2   Background and aims of the thesis

Mass infections of *T. crassus* are a well known and a widely documented problem for whitefish fisheries in North America, Europe and Russia (Miller 1952, Petersson 1971a,b, Kuperman 1973, Amundsen 1988). The parasite has great economic significance for fisheries since the occurrence of the plerocercoids in the muscles of the coregonids make the fish objectionable for human consumption. For example in the 1930-40's Canadian whitefishes were rejected from United States fish markets because of heavy infections of the parasite (Miller 1952).

In Finland *T. crassus* has a fragmented spatial distribution. It has been documented from whitefishes and vendace (*Coregonus albula* (L.)) in the Bothnian Bay, the Baltic Sea (Valtonen et al. 1989); and from whitefishes and pike from lakes in the watershed areas of two rivers in northeast Finland (Rintamäki 1989, A. Karvonen & E. T. Valtonen *pers. com.*). At the end of the 1980's, local fishermen reported the whitefish in Lake Saimaa, a large complex of lakes in southeast Finland belonging to the watershed area of River Vuoksi, to be heavily infected with *T. crassus*. According to the local fishermen the parasite had been present in the northern and central parts of the drainage area for a couple of decades (Karjalainen & Turunen 1991), but mass infections had

not been reported earlier. The problem emerged soon after the vendace populations had declined in most parts of the Lake Saimaa area. Vendace stocks exhibit strong natural fluctuations in Scandinavian lakes due to variations in year-class strengths. In different lakes, abundant year classes may occur regularly every other year or irregularly with several successive weak year classes (e.g. Viljanen 1986, Helminen et al. 1993). The study on parasite assemblages of whitefish in three study areas at Lake Saimaa in 1991 revealed that the level of *T. crassus* infection differed between the basins, such that whitefish were much less infected with *T. crassus* in one area where the vendace population had remained dense than in the other two areas where the vendace stocks had declined. This raised the question of the effect of local characteristics of the lake on the one hand and the effect of the density of vendace populations on the other hand on the transmission of *T. crassus*. Another aspect connected to the *Triaenophorus* problem in public discussion in one part of the lake was the abundant stocking of the dense gill-rakered whitefish type, *C. l. pallasi*, in the area. Elucidating the mechanisms affecting the transmission would contribute to the understanding of why *T. crassus* is present in some lakes but not in others and why its occurrence usually involves heavy infections in second intermediate hosts. Clarifying the patterns of accumulation of plerocercoids in whitefish would give an insight to the transmission mechanisms and also the impact of the parasite on the host populations.

One potential factor affecting the transmission of parasites through host species is the food competition between sympatric hosts. This kind of situation might be found between the coregonid hosts of *T. crassus*, whitefish and vendace, with regard to planktonic food. The knowledge on the feeding preferences of whitefish and vendace (e.g. Nilsson 1960, Svärdson 1976, Jacobsen 1982, Hakkari et al. 1985, Sandlund et al. 1985) and the circumstantial evidence on the abundances and growth of whitefish in the absence and presence of abundant vendace stocks (e.g. Heikinheimo-Schmid 1992, Valkeajärvi 1992, Salojärvi 1992) provide evidence for the status of vendace as a superior competitor for planktonic food able to displace whitefish from feeding on plankton. The strong fluctuations in the abundance of vendace populations and consequent changes in the strength of the food competition between whitefish and vendace might affect the transmission of parasites through planktonic and benthic food to whitefish. In addition to *T. crassus*, the occurrence of a swimbladder nematode *Cystidicola farionis* Fischer, transmitted via an amphipod *Monoporeia affinis* Lindström (see Valtonen & Valtonen 1978) was also studied as an indicator of benthic feeding in whitefish. During the 6-year study period the vendace stock remained dense in one of the study basins and sparse in another, while it increased from sparse to dense in the third area.

In order to verify the hypothesis on food competition between whitefish and vendace it became necessary to clarify which copepod species act as first intermediate hosts for *T. crassus* at Lake Saimaa. Different copepod species act as hosts in different geographical areas (Watson & Price 1960, Michajlow 1962, Kuperman 1973) but they have not been earlier determined from Finnish waterbodies. In the course of the field studies also the question about the host specificity of *T. crassus* with regard to the second intermediate hosts was raised,

which needed to be solved by experimental infections. For experiments a pure culture of *Cyclops strenuus* Fischer, a copepod that was found to become easily infected with *T. crassus*, was established and maintained in the laboratory. The high level of infection in whitefish indicated a high transmission efficiency from copepods to fish despite the temporally narrow transmission window, which led to the question of whether the parasite is actively manipulating copepod behaviour in order to enhance its own transmission. Interactions of *T. crassus* with one of its hosts, *Cyclops bicuspidatus thomasi* Forbes, have been previously studied in Canada (Rosen & Dick 1983, Shostak et al. 1984, Shostak & Dick 1985, Shostak et al. 1985), but the effect of *T. crassus* on the behaviour of copepods has not been studied. In the course of the work some results contradictory to the earlier findings on the effect of the parasite on the copepod host were found and therefore interaction of *T. crassus* with *C. strenuus*, including factors affecting the encounter between copepods and coracidia, were studied further.

2 MATERIALS AND METHODS

2.1 Study area (I, II, III)

The three study areas are situated in Lake Saimaa in southeast Finland, belonging to the watershed area of River Vuoksi. Southern-Saimaa (referred as area A) is situated in the main flow of the watercourse, while Lakes Puruvesi (area B) and Naistenvesi (area C) lie aside from the main water flow (Fig. 2). More detailed characteristics of the areas are provided in paper I.

The study areas differed from each other with regard to the abundance of coregonid stocks. Two types of whitefish (referred to as subspecies in I) present in Lake Saimaa can be separated by the number of gill-rakers: *Coregonus lavaretus wartmanni* is the native lake spawning whitefish with less than 37 gill-rakers and it was abundant in all study areas throughout the study period. Plankton-eating whitefish *C. l. pallasi* has more than 47 gill-rakers. *C. l. pallasi* were stocked into area A since the early 1980's, such that it provided 31% of the whitefish catches in 1989, but after the number stocked was greatly reduced from the early 1990's, not more than 6% in 1992 (Parkkonen 1993). After 1992 only a few *C. l. pallasi* were present in the whitefish samples from area A. In areas B and C, *C. l. pallasi* has been stocked sporadically in small numbers and it was not distinguishable in the catches. Only *C. l. wartmanni* was included in the study in papers II-III and it was referred to as *C. lavaretus* L. s.l. The strengths of the vendace (*C. albula*) stocks varied in the three study areas due to natural fluctuation in year-class strengths as described in paper II.

2.2 Field data (I, II, III)

Whitefish were collected from 1991 to 1996 annually. A total of 725, 621 and 317 whitefish were studied from areas A, B and C, respectively. The material

consisted mostly of *C. l. wartmanni* (<37 gill-rakers). The material from area A included 79 *C. l. pallasi* (> 47 gill-rakers) caught in 1991-1992 from the same samples as *C. l. wartmanni*. The few fish with gill-raker numbers between 37-47 were excluded from analyses as well as the few *C. l. pallasi* caught from areas B and C or from area A after 1992. A total of 227, 175 and 499 vendace were studied between 1991-1995 from areas A, B and C, respectively.

The fish and their parasites were studied as described in papers I, II and III. The age and back-calculation of whitefish lengths at age were determined from scales. For vendace, only the range of the age distribution was examined by determining the age of ca. 20 specimens at both ends of the length distribution.

In order to determine which species of copepods suitable as intermediate hosts for *T. crassus* occur in the study areas and in the diets of the second intermediate hosts, plankton samples and stomach samples from whitefish and vendace were collected concurrently from each of the three study areas (II).

2.3   Experimental infections (II, IV, V)

Mature *Triaenophorus* spp. were obtained from spawning pike at Lake Saimaa in southeast Finland from 1992 to 1997 and Lake Kostonjärvi in northeast Finland from 1996 to 1997 after ice-out each year. Eggs were obtained from mature worms as described in papers II, IV and V. Coracidia of *T. crassus* were used in all other experiments except for the photobehaviour experiment in IV and alternative food and feeding rate experiments in V, where mixtures of *T. crassus* and *T. nodulosus* coracidia were used.

In order to determine which copepod species are suitable as first intermediate hosts for *T. crassus*, copepods were collected from Lake Saimaa and exposed to *T. crassus* coracidia in the laboratory (II). In addition *Eucyclops serrulatus* and *Cyclops strenuus* from pure cultures initiated from identified egg-bearing females obtained from lakes situated near Jyväskylä were exposed.

All other experimental infections of copepods and fish were made using *C. strenuus* originating from the pure culture maintained in the laboratory. The procedures for infecting the copepods are given in papers II, IV and V. The copepods were screened for the developmental stage and infection status immediately before the experiments.

One-month-old whitefish and vendace used in the infection and predation experiments were obtained from two commercial farms near Jyväskylä. The procedures for maintaining and exposure of the fish were given in papers II and IV. The exposed fish were examined for *T. crassus* plerocercoids while fresh. The few fish that died during the experiments were checked similarly and included in the results, since the infection was detectable already at day 1 postinfection.

2.4   Terminology (I-V)

Terminology used in this thesis and the original papers follows those outlined by Margolis et al. (1982) (I) and Bush et al. (1997) (II-V). Prevalence of infection is the percentage of hosts (copepods or fish) infected and mean abundance (abundance in I) is the mean number of parasites per hosts examined. Infection intensity refers to the number of parasites in any infected host and mean intensity is the mean number of parasites per infected hosts. All parameters above refer to a given parasite species. In the case of experimental infections the terms exposed and postexposure (p.e.) refer to all hosts exposed to the parasite whether they became infected or not and the terms infected and postinfection (p.i.) to those that became infected following exposure. Parasite infra-community (I) includes all parasites within a single fish host (Bush et al. 1997).
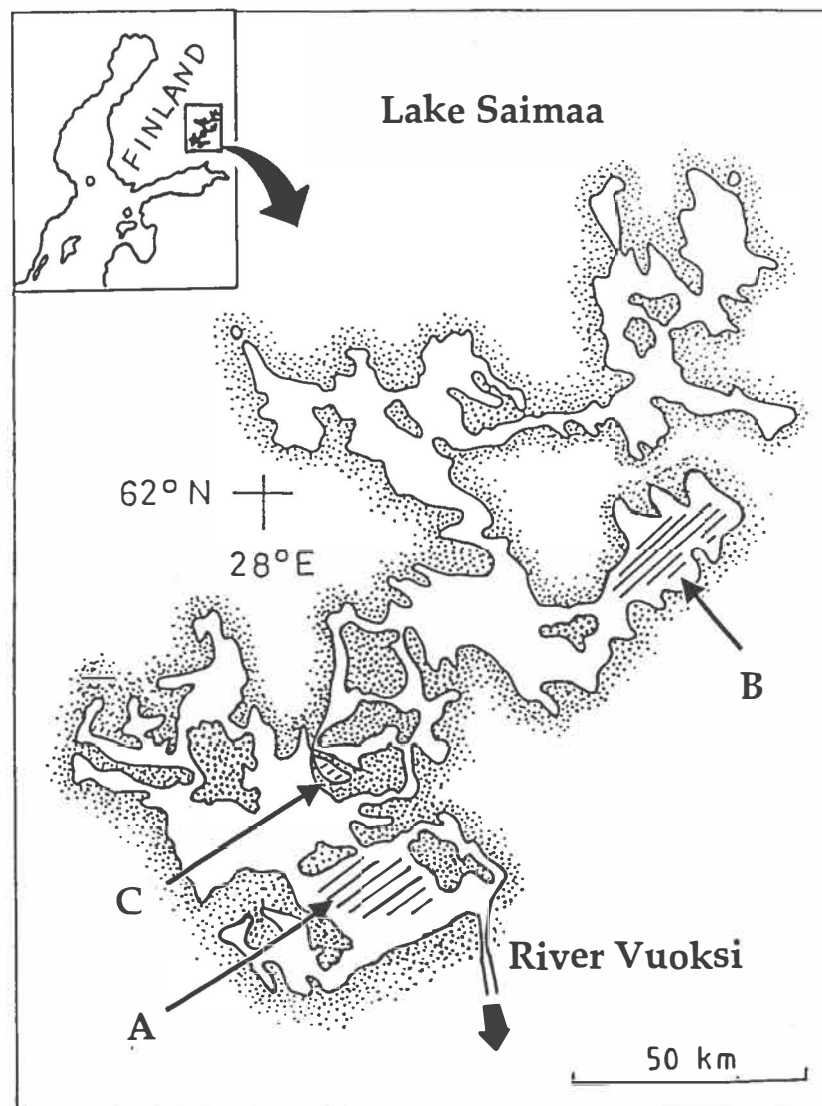

FIGURE 2   The study area. A = Southern Saimaa, B = Puruvesi and C = Naistenvesi. Broad arrow indicates the flow direction of River Vuoksi.

3 RESULTS AND DISCUSSION

3.1 Factors affecting transmission of *T. crassus*

3.1.1 Encounter between coracidia and copepods (V)

The availability of alternative prey to coracidia was found to affect the success of cestode transmission to the first intermediate hosts (V). Copepods exposed to the same number of coracidia harboured considerably fewer procercoids in the trials where ciliates or one-day-old *Artemia salina* nauplii were simultaneously offered as alternative food items. It appeared that the copepods preyed on ciliates and coracidia as encountered and could not distinguish coracidia from ciliates, but a preference for *Artemia* over ciliates could not be proven.

The proportions of infected copepods were found to differ between the developmental stages, such that copepodite V stages were infected around four times more frequently than copepodite IV stages and the prevalence of infection in adult specimens was higher than in copepodites. This corresponds to the expectation that the number of coracidia acquired by an individual copepod depends on encounter and ingestion rates of coracidia, which are higher in larger than in smaller individuals due to their higher swimming and foraging ability (Nie & Kennedy 1993, Wedekind 1997). However, the probability of infection is not determined by size only, since although they are smaller, males had a slightly higher prevalence than females. This is probably explained by the higher susceptibility to infection in males (Wedekind & Jakobsen 1998). The results of different studies on the probability of different developmental stages to acquire infection seem to depend also on the exposure time, such that with an increase in time, the probability of infection in small copepodites is increased (Kuperman & Kireev 1976, Dupont & Gabrion 1987, Nie & Kennedy 1993).

These results indicate that acquisition of coracidia by copepods depends not only the concentrations of parasites and hosts, but also on the presence of alternative prey for copepods and on the host population dynamics.

3.1.2 Encounter between copepods and fish (I, II)

Parasites have been widely used as biological indicators or tags to provide information on various aspects of host biology and ecology including their diet and feeding behaviour (Williams et al. 1992, Arthur 1995). Parasite assemblages in whitefish populations in the three study areas in Lake Saimaa were used as indicators of whitefish behaviour and local area characteristics and their effect on the transmission of *T. crassus* (I). The parasite assemblages of whitefishes were predicted to be affected by the ecology of the whitefish type, such that *C. l. pallasi* with a higher gill-raker number was expected to harbour more parasites transmitted via planktonic food and less parasites transmitted via benthic food than *C. l. wartmanni* with a lower gill-raker number and *vice versa*. However, the parasite assemblages were found to differ more between the *C. l. wartmanni* populations in the three study areas than between the two whitefish types in area A (I). This implied that the local characteristics of the habitat, such as amount of littoral areas, were more important in modifying the structure of parasite populations than differences in gill-raker number between the whitefish types.

Nevertheless, some differences were found between the two whitefish types in area A in the proportion of parasites transmitted via planktonic or benthic food. *C. l. pallasi* harboured more *Diphyllobothrium dendriticum* transmitted via planktonic copepods and less *Cystidicola farionis* transmitted via benthic amphipods than *C. l. wartmanni*, which seemed to confirm the more planktonic diet of *C. l. pallasi* (I). However, *C. l. pallasi* harboured less *T. crassus* than *C. l. wartmanni*. Neither was there any general correlation between the occurrence of the two cestodes in either whitefish type (I). *C. l. pallasi* had been stocked in the lake as one-summer-old juveniles. When compared to those *C. l. wartmanni* that had experienced a similar number of *T. crassus* invasions, the mean abundances and variance to mean ratios were lower for *C. l. pallasi*, showing a lower accumulation of the parasite, although the differences in prevalences and mean abundances were not statistically significant (Table 1). This was unexpected, because heavier infections of plankton-feeding cisco when compared to whitefishes (Miller 1952), and of dense gill-rakered plankton-feeding whitefish when compared to sparsely gill-rakered benthos-feeding whitefish (Petersson 1971a,b, Amundsen 1988), have suggested a connection between the planktonic feeding mode and the intensity of *T. crassus* infection. In Lake Saimaa the role of dense gill-rakered *C. l. pallasi* in the maintenance of *T. crassus* seems less important than that of *C. l. wartmanni*, however, taking into account their slightly lower parasite burden and their low proportion of the whitefish stock in the area. In Swedish lakes pelagic dense gill-rakered whitefish were found to live at a greater depth in spring than whitefish with a lower gill-raker number (Petersson 1971a). If a similar situation is true for *C. l. pallasi*, it might be less exposed to *T. crassus* than *C. l. wartmanni* in spite of its generally more planktonic diet which in turn exposes it more to *D. dendriticum*, which is transmitted via pelagial copepods throughout the summer (Henricson 1978).

TABLE 1   The prevalences (%), mean abundances (abund.) ± s.d. and variance to mean ratios (s^2/x) of *Triaenophorus crassus* infection in *Coregonus lavaretus pallasi* within age groups in area A in 1991-1992. Statistical comparisons (G-tests and Mann-Whitney U-tests for prevalence and mean abundance, respectively) were made with *C. l. wartmanni* that had been exposed to an equal number of *T. crassus* invasions as *C. l. pallasi* stocked as one-summer-old juveniles. N=number of fish studied. **$p<0.01$, *$p<0.05$, NS not significant.

		C. l. pallasi					C. l. wartmanni					
Year	Fish age	%	abund.	s^2/x	n	Fish age	%	abund.	s^2/x	n	%	abund.
1991	3	73.3	1.7±2.0	2.3	15	2	40.9	1.3±2.3	4.3	44	*	NS
	4	60.0	1.4±1.5	1.6	15	3	80.5	3.4±2.9	2.5	123	NS	**
	5	88.9	2.5±2.1	1.8	18	4	87.5	4.0±4.0	4.0	80	NS	NS
	6	85.7	2.7±1.8	1.2	7	5	93.7	5.0±3.7	2.8	63	NS	NS
1992	6	100.0	3.7±1.0	0.3	9	5	100.0	5.5±3.0	1.7	12	NS	NS

The effect of potential competition on planktonic food between whitefish and vendace on the transmission of parasites to whitefish was studied by comparing the abundances of *T. crassus* and *C. farionis* in whitefish populations in Lake Saimaa, excluding *C. l. pallasi* (II). If vendace displaces whitefish from feeding on plankton this should be seen in the transmission and consequently as differences in the abundance of those parasites in whitefish in areas with different levels of vendace stocks.

The results obtained from the level of *C. farionis* infection in whitefish in areas B and C seemed to confirm the expectation, but in the case of *T. crassus* the prediction held true only partially. After 1993 the level of *T. crassus* infection increased in areas C and A despite the high density of the vendace stocks. Only 0.2% of vendace in Lake Saimaa were found to harbour *T. crassus* (II), which seemed to contradict the idea about the competition between whitefish and vendace on copepods transmitting *T. crassus*. However, in further experiments the copepod species occurring in Lake Saimaa which act as first intermediate hosts of *T. crassus* were clarified and their occurrence in the stomach samples of both whitefish and vendace was verified (II). In experimental infections vendace did not become infected with *T. crassus* but whitefish did (II).

Thus, the strength of vendace population seemed to have some effect on the abundance of *C. farionis* infection in whitefish, but not so in the case of *T. crassus*. The reason for this is possibly the synchronization of *T. crassus* transmission with the seasonal feeding activity of coregonids. Copepods are abundantly available for both whitefish and vendace in the littoral areas in spring, which ensures the transmission of *T. crassus* to whitefish despite the abundance of vendace stocks competing for planktonic food. Vendace, on the other hand, do not become infected, due to their lower infectivity. Later in the summer competition may force whitefish to shift from planktonic to benthic

food, which includes amphipods transmitting *C. farionis*. However, in lakes where vendace stocks have declined, whitefish may continue to feed on plankton throughout the summer and avoid exposure to *C. farionis*.

In area C the low level of *T. crassus* infection in whitefish in 1991-1992 could have been caused by the lake morphology affecting the abundance of littorally transmitted parasites (I). On the other hand, after 1993 the abundance of *T. crassus* in the area increased considerably (II). It is also possible that the parasite had invaded this area later than the other two areas. The movement of whitefish to the area C is restricted with the narrow, shallow opening of the area to the other parts of Lake Saimaa (I), which may have slowed the invasion of the parasite to the area. The continuous rise in numbers of *T. crassus* in whitefish is consistent with the establishment of a *T. crassus* population into this isolated part of the Saimaa lake complex. In subsequent years the parasite established a reservoir in the whitefish which led to an increase in the infection to the same level as in the other two areas.

In area A the decrease in the mean abundance of infection in 1993 (II) may have been caused by a temporary failure in the transmission of *T. crassus* due to unusual weather conditions in spring and early summer. The surface water warmed up very rapidly in the second week of May up to 14 °C and then cooled rapidly down to 7 °C during the last part of May due to strong northerly winds that disrupted the stratification and mixed the waters again. Rapid fluctuation in temperature may have affected the development of *T. crassus* eggs, the development of the copepod population in the littoral zone or the movements of whitefish, and therefore hindered the encounter between infected copepods and whitefish. The importance of abiotic factors has been shown to be crucial in determining the transmission success of *T. crassus* in Canada, where the distribution of *T. crassus* has been observed to depend on the temperature isotherm (so called Kennedy's line), south of which the littoral area warms in the spring rapidly and causes the coregonids to leave the area too early to contact infected copepods (Lawler & Scott 1954).

3.1.3 Parasite-induced changes in copepod behaviour (IV, V)

Infection with *T. crassus* procercoids caused alterations in the feeding behaviour (V), activity and microhabitat selection (IV) of the first intermediate host *C. strenuus*. Infection also increased the susceptibility of the copepods to be eaten by the second intermediate host *C. lavaretus* juveniles in laboratory experiments (IV). The increased susceptibility to predation was probably caused by the changes in the behaviour of the infected copepod, which made it more conspicuous to and/or easier to catch by a fish predator.

Only a few cases of parasite-induced changes in host behaviour have been shown to increase parasite fitness and therefore be likely to represent parasite adaptations (Moore & Gotelli 1990, Combes 1991a, Poulin 1994, 1995). An adaptation is a genetically determined trait that confers a selective advantage upon the organism and thus spreads in the population (Ridley 1993). Apart from parasite adaptations, changes in host behaviour might be adaptive also for

the host, or in the simplest case, non-adaptive side effects of infection (Minchella 1985). In case of *T. crassus* the evidence for active manipulation of the copepod host is equivocal and the significance of the behavioural alterations to the fitness of the parasite and thus their adaptive value remains unclear.

The behavioural alterations were detected in experiments with 12-day-old or older procercoids, but not in experiments with 10-day-old procercoids. In experimental infections of whitefish juveniles, the fish exposed to 10-day-old procercoids did not become infected but those exposed to 12, 14 or 21 days old procercoids did (IV). These results could mean that *T. crassus* procercoids cause behavioural alterations in the copepod host only after they have become infective to the next host. This could be a sign of active manipulation of the host adaptive to the parasite (Bethel & Holmes 1974, Poulin et al. 1992, Poulin 1995). However, since the behavioural experiments with 10-day-old procercoids were made in another year and a partly different procedure was used in the predation experiment, the results are not directly comparable to those from the experiments with older procercoids.

Although *T. crassus* was found to increase the susceptibility of an infected copepod to whitefish juveniles in the laboratory, parasitic infection might increase the copepods susceptibility also to predation by planktivorous fish other than whitefish, which would not be adaptive for the parasite (Moore & Gotelli 1990, Poulin 1995). Moreover, the behavioural changes caused by *T. crassus* seemed to be fairly simple quantitative changes in the normal behaviour, which are more likely to be caused by simple pathological reactions of infection or to have arisen by chance as by-products of other selective pressures, than some more complex changes in the behaviour of the host (Moore & Gotelli 1990, Poulin 1995). However, in the case of cestode-copepod systems the costs and complexity of the underlying mechanisms causing the altered behaviour (Helluy & Holmes 1990, Poulin 1995) are not known.

The magnitude of the alterations in the swimming behaviour of copepods infected with *T. crassus* were independent of the number of procercoids (IV). This could be an evidence of the active manipulation of the host by the parasite, since behavioural changes could be expected to be independent of the infrapopulation size in parasites that usually occur in single infections (Poulin 1994), such as tapeworm procercoids in their copepod hosts (Watson & Lawler 1965, Boyce 1974, Hanzelova 1992). Moreover, if changes in the behaviour of infected hosts were caused by pathological side effects of infection, the intensity of the alteration could be expected to increase with the number of procercoids within a host. On the other hand, the pathological effect might be associated with the biomass of the parasite relative to that of the host, which could be relatively independent of the number of procercoids within a host due to density-dependent processes in procercoid growth (Rosen & Dick 1983, Shostak & Dick 1985).

Similar behavioural changes induced by phylogenetically unrelated parasites might be an indication of convergent evolution under similar selective pressures and thus evidence for parasite adaptations which had arisen independently (Poulin 1995). In related taxa similar changes may be a sign of common ancestry. Increased activity in copepods infected with cestode

parasites has been recorded in all studied copepod-cestode systems, including the present one (Poulin et al. 1992, Urdal et al. 1995, Wedekind & Milinski 1996), except for the work of Pasternak et al. (1995), where a decrease in activity of infected copepods was found. In the work of Pasternak et al. (1995) the copepods were collected from nature and thus the age of the infection was not known as in the experimental infections in the other works. The contradictory results in the work of Pasternak et al. (1995) might have been a result of different timing of observation as compared to other works. Also C. *strenuus* infected with T. *crassus* became more sluggish and easier to catch by pipette with the increase in the age of the infection. Different species of cestode procercoids seem therefore to elicit similar alterations in the behaviour of infected copepods, which may be due to common ancestral inheritance. However, this does not necessarily foil the adaptive value of the alterations (Thomas & Poulin 1998).

3.1.4   Host specificity (II)

Host specificity of a parasite is the outcome of the interaction between parasite and host genomes (Combes 1991b, Janovy et al. 1992). In order to continue its life cycle, a parasite must be precisely adapted to the structural, physiological and immunological features of the host species (Wakelin 1984). The range of potential hosts for a certain parasite is a continuum from those in which the parasite never becomes established, through those in which the parasite may become established but will not develop, to those in which it develops best (Holmes 1979). The range of host specificity varies from a near absolute restriction for one host species or family to a wide array of different hosts (Holmes 1983). For the majority of parasites host specificity falls between the two extremes and under natural conditions particular species are found in only a few species of hosts (Wakelin 1984).

Reaching a suitable host is of primary importance in determining the fitness of a parasite. Therefore parasites transmitted passively through food webs should face strong selection pressure to increase the probability of reaching hosts in which they can develop and to develop in those they regularly reach (Holmes & Price 1986). Changes in the host community may lead to changes in the reciprocal selective pressures exerted between host and parasite, which in turn may lead to coevolutionary changes in gene frequencies in microevolutionary time (Holmes 1983). Passage through a new host has been shown to alter the infectivity of a helminth for a new host (Laurence & Pester 1967) or the old one (Saoud 1965). Continued association with a given host species is likely to select for such parasite genotypes that are compatible with that host. Increases in the relative population of that host would be likely to increase these selective pressures and conversely, any factor that reduces the relative population size of a major host would be likely to reduce them (Holmes 1983). Alteration of host community structure, therefore, would be expected to affect the coevolutionary selection patterns of a parasite having substantial populations in more than one species. A host species that is rarely infected, that

is infected with few individuals, or which does not transmit the parasite further, would not be important in selection for traits of that parasite. Coevolution with one species of host could be extensive even if the parasite had a wide array of hosts, presuming that the majority of the parasites that contribute to the continuation of the life-cycle are found in that host species (Holmes 1983).

In Lake Saimaa whitefish was found to be heavily infected with *T. crassus* (I, II, III), while vendace was found to be only accidentally infected (II). Of the 901 vendace studied only two infected vendace were found (0.2%), both harbouring a single parasite. In the experimental infections vendace did not become infected with *T. crassus*, while whitefish were infected successfully (II). These results indicate a lower infectivity of *T. crassus* for vendace than for whitefish in Lake Saimaa area. In Bothnian Bay and Swedish Lakes whitefish have been found to be more heavily infected with *T. crassus* than vendace (Valtonen et al. 1989, Petersson 1971b), while in Lake Ladoga and Rybinsk reservoir vendace is the primary second intermediate host (Kuperman 1973). The importance of whitefish and vendace as second intermediate hosts for *T. crassus* seems to vary in different areas. This might be caused by differences in the host community structures exerting coevolutionary pressures on *T. crassus* populations in different areas.

Adaptation to hosts that the parasite regularly meets is seen also in the host specificity of *T. crassus* towards the first intermediate copepod hosts. The copepod species that *T. crassus* infects are those that occur regularly in large numbers at the time when the infective stages of *T. crassus* are present in the lake and which thus are exposed to the parasite. Experimental infections showed that the copepod species present in littoral areas of Lake Saimaa that were suitable as intermediate hosts for *T. crassus* belonged to the genera *Eudiaptomus* and *Cyclops* (II), that occur commonly in the littoral zone in early summer (Latja 1974, Hakkari 1978, Sarvala 1979). On the other hand two common cyclopoid species *Thermocyclops oithonoides* and *Mesocyclops leuckarti*, which are more pelagial and that have their population peaks later in the summer (Hakkari 1969, Poikolainen 1970, Latja 1974) were unsuitable as hosts for *T. crassus* as has been previously found by Kuperman (1973). Also calanoid species *Heterocope appendiculata* and *Eurytemora lacustris*, which are not abundant in spring (Hakkari 1978), are not suitable as hosts for *Triaenophorus* spp. according to Kuperman (1973).

3.2 Effects of *T. crassus* on hosts

3.2.1 Effects on copepods (IV, V)

The parasite uses the host as a resource for its own maintenance and reproduction and therefore can adversely affect the fitness of the host by decreasing host fecundity and/or survival (e.g. Dobson 1988, Barnard 1990, Hurd 1990). Fecundity and survival may be affected directly via the pathology caused by the parasite on the vital organs or indirectly due to changes in the

behaviour of the host (Holmes & Zohar 1990). One important factor contributing to the fitness components of the host is its nutrition. Parasites may compete with the host for energy or nutrients or increase the host's energy demand by damaging its tissues. Assimilation efficiency of the host may be affected directly or through tissue damage. Host food intake may be affected as well, either by a voluntary decrease in the food intake or by the pathology caused by the parasite (Holmes & Zohar 1990). Parasites have been shown to modify feeding patterns of their intermediate hosts (Milinski 1990, Moore & Gotelli 1990). The host may try to compensate for the increased nutritional demands caused by the parasite with increased foraging (Milinski 1985, Holmes & Zohar 1990).

In *C. strenuus, Triaenophorus* infection decreased the feeding rate of copepods to almost zero during a seven-day observation period p.i. while in uninfected copepods the feeding rate remained stable (V). The result is similar to that observed by Pasternak et al. (1995) in *Cyclops* infected with *Diphyllobothrium* spp., but on the other hand, Shostak & Dick (1985) did not find any effect of *T. crassus* infection on the feeding of copepods on *Paramecium*. These three studies, including the present one, are the only cases where the food intake in infected copepods has been studied. These results may indicate that cestode infection affects copepods' ability to catch and handle large prey such as *Artemia* nauplii, rather than the copepods' ability to ingest and digest food, but more systematic studies are needed to verify this.

T. crassus infection was found to affect both survival and fecundity of *C. strenuus* (V). The frequency of infected females carrying egg sacs was found to be strongly reduced as compared to uninfected females and the survival of infected copepods was lower than that of uninfected ones. Fecundity and survival of exposed but uninfected copepods did not differ from that of unexposed copepods. These results are contradictory to the results obtained in earlier studies on the effect of *T. crassus* infection on *C. b. thomasi* (Shostak & Dick 1985, Rosen & Dick 1983). Allowing for species specific differences in the interactions, the differences in the results on the effect of the parasite on copepod survival may be due to differences in the infection intensities of copepods in the experiments and the duration of the observation period post-exposure. This is discernible also in studies with other copepod-cestode systems (Rosen & Dick 1983, Shostak & Dick 1985, Nie & Kennedy 1993, Pasternak et al. 1995, Wedekind 1997). The differences in the results on the effect of infection on copepod fecundity might be due to differences in the feeding regimens of copepods in the experiments (Shostak & Dick 1985), which would affect the energy available for both the copepod and the parasite. Wedekind (1997) has suggested that the reduced frequency of egg production in infected females might also be due to an earlier start of reproduction in infected than in uninfected females. Such life-history response to infection even at the cost of producing fewer eggs could be expected since the parasite infection would have a greater effect on future than on current reproduction (Forbes 1993).

In natural copepod populations tapeworm procercoids occur usually in single infections (Watson & Lawler 1965, Boyce 1974, Hanzelova 1992) and therefore the effects of the parasites are likely to be less severe or to develop

more gradually than in laboratory infections where higher intensities are usually involved. Parasite-induced changes that increased the copepod vulnerability to whitefish predation were discernible after 12 days p.i. (IV), while the effect on mortality was apparent only after three weeks p.i. (V). The fitness costs of *T. crassus* infection in natural populations of *C. strenuus* are therefore likely to be manifested primarily by decreased fecundity and increased mortality through predation rather than through a direct decrease in survival.

3.2.2 Effects on whitefish (III)

The effect of *T. crassus* infection on *C. l. wartmanni* was studied from field samples from areas A and B, where most representative samples were collected. Although almost all whitefish were infected, the bulk of the parasite population was nevertheless aggregated in a small proportion of the host population. Annual accumulation of parasites to whitefish differed between the study areas, such that in area A accumulation was approximately one parasite per year. In area B, where the overall level of infection in whitefish, measured as prevalence and mean abundance, was higher than in area A, there was a sharp increase in accumulation from 1.6 in the younger fish to 3-4 parasites per year in fish over 5 years of age. The increase in accumulation in area B was seen from the data within each of the years. This excludes the possibility that fish of 6 years and older experienced higher transmission rates in a period of 6 to 10 years prior to catch, since this would be seen as an increased mean abundance in consecutive age classes (within cohorts). This implies an existence of a threshold intensity after which the probability of acquiring further parasites is increased. Such threshold might be caused by a breakdown in the defence mechanisms of the whitefish (Nie et al. 1996), or by an increased energy demand due to heavy infection and consequent increase in food intake (Walkey & Meakins 1970, Milinski 1985, Giles 1987), which would in turn expose the fish to increased numbers of parasites even though the increased food intake is not seen in fish growth. In individual fish the threshold would depend on the fish's ability to compensate for the adverse effects of infection and it would likely vary between individuals depending on their general health (Holmes 1982, Holmes & Zohar 1990). If the plerocercoid infection impairs the swimming ability or stamina of infected fish and thus its ability to catch planktonic items, previous infection might also increase the fish's exposure to infected copepods that are easier to catch than uninfected ones.

Direct comparisons between the mean lengths and weights of uninfected and infected whitefish from Lake Saimaa did not reveal any effect of the parasite on whitefish growth as has been earlier found by Miller (1945) on whitefish (*C. clupeaformis*) and cisco in Canada. However, back-calculation of fish lengths at age and correlational data both indicated that old infected fish were smaller than uninfected ones, while in young fish the reverse was true (III). Both of these patterns might have been caused by a situation where younger larger fish ate more plankton and had a higher exposure to *T. crassus*

than smaller fish after which their growth was slowed down due to increased parasite load. In young 2 to 4-year-old fish the annual increase in mean abundance was not correlated with the mean annual weight increase. The effect of infection on growth of the whitefish seemed therefore to be concentrated in the oldest fish which harboured most of the parasites.

In spite of the heavy aggregation of parasites in the older fish, no evidence on the effect of parasite-induced mortality was found from infected fish from Lake Saimaa. In area B the variance to mean ratios and mean abundances seemed to level off in the oldest age groups. This pattern might have been caused by the small sample sizes in the oldest age groups (Pacala & Dobson 1988), or by a parasite mortality which exceeded their recruitment in the oldest hosts (Anderson & Gordon 1982, Kennedy 1984). Previous estimates on the life span of *T. crassus* have been based on the increase in frequency of degenerated cysts in older fish (Miller 1952). However, according to histological studies the degeneration of *Triaenophorus* cysts seems to depend on the host's ability to mount an immunological response rather than on cyst age (Rosen & Dick 1984, Hoffmann et al. 1986). Degenerating cysts were also observed in this study and were included in the plerocercoid count, but their occurrence seemed to be independent of fish age. Therefore it is likely that *T. crassus* plerocercoids accumulated through the life span of the host are detectable from their muscles. Possibly any decrease in variance to mean ratio in the oldest hosts was not detected because the probability of acquiring more parasites increased with increasing existing parasite load (and age), as seemed to be the case in area B.

Parasite-induced reduction in growth of the host is likely to be coupled with a reduction in the reproductive output of the host. In this work the effect of *T. crassus* infection on the fecundity of the whitefish was not studied. However, since the effects of *T. crassus* infection on the growth of the whitefish were concentrated in the oldest hosts, the possible impact of *T. crassus* on the reproduction of the whitefish populations is likely to be less severe than if the effects on growth had been seen already in young (2 to 5 years old) fish, which constitute a larger part of the population and contribute to its reproductive output more than the older fish.

4   CONCLUSIONS

The results of this thesis suggest that the heavy infections of *Triaenophorus crassus* found in whitefish in Lake Saimaa are the combined outcome of 1) the high transmission efficiency due to the synchronisation of transmission into the ecology of the hosts, 2) possible parasite-induced behavioural changes in the copepod host which increase their susceptibility to fish predation and 3) the accumulation of the plerocercoids with fish age 4) coupled with the possible increase in the probability of acquiring further parasites after a certain threshold intensity has been achieved.

The abundance of vendace (*Coregonus albula*) stocks did not affect the level of *T. crassus* infection in whitefish (*C. lavaretus* s.l.) at Lake Saimaa. The existence of food competition between whitefish and vendace was, however, implied by the higher abundances of *Cystidicola farionis* transmitted via benthic amphipods in whitefish in the area where the dense vendace stock may have displaced whitefish from feeding on plankton. Possibly the synchronization of the transmission of *T. crassus* into the seasonal feeding behaviour of coregonids ensures the transmission of the parasite to whitefish in the littoral zone in spring. At this time of the year copepods are abundantly available for both whitefish and vendace, which gives whitefish an opportunity to eat enough infected copepods for the transmission to occur irrespective of the density of the vendace population. However, the amount of plankton included in the diet was not directly connected to the level of *T. crassus* infection. Dense gill-rakered *Coregonus lavaretus pallasi* was found to accumulate *T. crassus* slightly less than sparse gill-rakered *C. l. wartmanni*, which is possibly explained by the more pelagial feeding habits of the former type. Vendace, which is an obligate plankton feeder and the primary host of *T. crassus* e.g. in Lake Ladoga, was found to be infected only accidentally in Lake Saimaa and in experimental infections vendace did not become infected with *T. crassus*. The host specificity of *T. crassus* with regard to vendace in Lake Saimaa seems therefore to differ from that observed elsewhere in northern Europe and may reflect different coevolutionary pressures in different areas.

T. crassus was found to induce behavioural changes in the first intermediate copepod host (*Cyclops strenuus*) and to make it more susceptible to

whitefish predation. However, the significance of the behavioural changes to the fitness of the parasite and thus their adaptive value remained unclear. Thus the behavioural alterations in copepods were not necessarily caused by active manipulation by the parasite. In copepods, infection levels higher than those probably encountered in nature did not affect the survival of the copepod until well after the parasite had become infective to the next host. In natural populations the infected copepods are therefore likely to be preyed upon before the direct lethal effects of parasitism are developed. The parasite affected the copepod fecundity, which might have consequences for the population dynamics of the copepod.

Whitefish in Lake Saimaa were frequently infected with *T. crassus* plerocercoids. Back-calculation of fish lengths and correlational data both indicated that old infected fish were smaller than uninfected ones, while in young fish the reverse was true. This pattern may have been generated by a situation where younger larger fish ate more plankton and had a higher exposure to *T. crassus* than smaller fish, after which their growth was slowed down due to increased parasite load. The effects of *T. crassus* infection on the growth of the whitefish seemed to be concentrated in the oldest hosts, but no evidence of parasite-induced mortality was found.

The transmission event from the final host to whitefish is nevertheless sensitive to disturbances, as shown by the decrease in the transmission of the parasite in area A in 1993, which was possibly caused by unfavourable weather conditions, which may have affected the encounter between coracidia, copepods and fish. Only certain copepod species act as first intermediate hosts for *T. crassus* and their population dynamics and the amount of alternative food to coracidia available for copepods are likely to affect the transmission efficiency. These factors coupled with the narrowness of the transmission window may thus determine the invasion success of the parasite. Possibly several successful transmission events are required for the establishment of the life cycle of the parasite in a lake. Once the parasite has been established in an area, however, the incorporation of the transmission into the ecology of the hosts and a plerocercoid reservoir in the second intermediate hosts maintain the high transmission efficiency of the parasite.

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YHTEENVETO

Haukimadon (*Triaenophorus crassus*) siirtyminen hankajalkaisista siikakaloihin ja loisen vaikutukset väli-isäntiin

Väitöskirjatyössäni tutkin haukimadon (*Triaenophorus crassus*) esiintymistä 2. väli-isännissään siioissa (*Coregonus lavaretus* L. s.l.) ja muikussa (*C. albula*) kolmella tutkimusalueella Saimaalla vuosina 1991-1996, sekä loisen siirtymiseen 1. väli-isännistä hankajalkaisäyriäisistä 2. väli-isäntiin siikakaloihin vaikuttavia tekijöitä. Haukimatoa esiintyi siialla kaikilla tutkimusalueilla. Loisen esiintyminen ei kuitenkaan ollut suorassa suhteessa planktonin syöntiin, koska planktonia syövällä tiheäsiivilähampaisella (>47 sh) siikatyypillä (*C. l. pallasi*) loista esiintyi hieman vähemmän kuin harvasiivilähampaisella (<37 sh) tyypillä (*C. l. wartmanni*). Yllättäen Saimaalta tutkitusta n. 900 muikusta haukimatoa tavattiin vain kahdesta yksilöstä (0.2%), vaikka esim. Ruotsin järvissä ja Laatokassa jopa 60% ja Perämerellä 8% muikuista on aiemmin todettu loisituiksi. Laboratoriokokeissa haukimato infektoi siikoja, mutta muikkuun loinen ei tarttunut.

Muikkukannan tiheys vaihteli luontaisesti Saimaan kolmella tutkimusalueella siten, että yhdellä alueella muikkukanta säilyi tiheänä ja toisella alueella vallitsi muikkukato koko tutkimusjakson ajan, kun taas kolmannella alueella muikkukanta elpyi tutkimusjakson aikana. Pohjalla elävän valkokatkan (*Monoporeia affinis*) mukana siirtyvän sukkulamadon (*Cystidicola farionis*) esiintyminen siioilla näytti korreloivan muikkukannan tiheyden kanssa. Havainto tukee oletusta, että muikku voi vahvana kilpailijana planktonin suhteen syrjäyttää siian syömästä planktonia ja pakottaa sen turvautumaan pohjaeläinravintoon. Heikon muikkukannan aikana siioille on puolestaan tarjolla runsaasti planktonravintoa, jolloin hankajalkaisäyriäisten välityksellä siirtyvän haukimadon määrän siioissa tulisi kasvaa. Haukimadon esiintyminen siioilla ei kuitenkaan näyttänyt korreloivan muikkukannan tiheyden kanssa. Siian ja muikun vatsansisältöjen analyysit vahvistivat, että molemmat lajit syövät hankajalkaislajeja, jotka laboratoriokokeiden mukaan voivat toimia haukimadon 1. väli-isäntinä. Tulokset vahvistavat käsitystä siitä, että haukimadon siirtymistehokkuus isännästä toiseen perustuu siihen, että sen siirtyminen ajoittuu tarkasti isäntien vuodenaikaisen käyttäytymisen kanssa. Loisen munat vapautuvat veteen pääisännän, hauen (*Esox lucius*), suolesta sen saapuessa kutemaan ranta-alueille keväällä jäiden lähdön jälkeen. Munista kuoriutuneet korakidiatoukat joutuvat hankajalkaisten ravinnoksi ja kehittyvät niiden ruumiinontelossa prokerkoidi-toukaksi. Loisitut hankajalkaiset joutuvat puolestaan keväällä ranta-alueelle ruokailemaan saapuvien siikojen ja muikkujen saaliiksi. Koska hankajalkaiset ovat tähän aikaan vuodesta ainoa runsaana esintyvä ravintokohde, siiat syövät muikkukannan vahvuudesta riippumatta tarpeeksi loisittuja hankajalkaisia infektoituakseen haukimadoilla. Vaikka muikkukin syö loisittuja hankajalkaisia, loinen ei tartu siihen yhtä herkästi kuin siikaan. Kesällä tiheä muikkukanta syönee planktonia niin tehokkaasti, että siika siirtyy syömään enemmän pohjaeläinravintoa ja infektoituu katkojen välityksellä siirtyvällä *C. farionik*sella. Kuitenkin alueilla, joissa on muikkukato,

siika voinee jatkaa planktonin syöntiä läpi kesän ja välttyä *C. farionis* - infektiolta.

Ensimmäisessä väli-isännässä *Cyclops strenuus* -hankajalkaisessa loisen prokerkoidi-toukka aiheutti muutoksia hankajalkaisen ravinnonotossa, pakenemiskyvyssä, uintiaktiivisuudessa ja mikrohabitaatin valinnassa. Loisitut hankajalkaiset olivat alttiimpia 0+ siikojen saalistukselle kuin loisettomat yksilöt. Käyttäytymismuutoksia havaittiin 12-16 vrk infektion jälkeen, mutta ei 10 vrk infektion jälkeen tehdyissä kokeissa. Altistuskokeissa siiat infektoituivat 12, 14 tai 21 vrk ikäisillä prokerkoideilla, mutta eivät 10 vrk ikäisillä loisilla. Tulokset viittaavat siihen, että haukimadon prokerkoidi aiheuttaa käyttäytymismuutoksia hankajalkaisessa vasta kun se on kehittynyt infektiiviseksi seuraavalle väli-isännälle. Kyseessä voisi tällöin olla isännän käyttäytymisen aktiivinen manipulointi loisen taholta oman siirtymisensä edistämiseksi. Käyttäytymiskokeet 10 vrk ikäisillä loisilla tehtiin kuitenkin eri vuonna kuin kokeet vanhemmilla loisilla, joten tulokset eivät ole suoraan verrattavissa toisiinsa.

Loisinta vaikutti myös *Cyclops strenuuk*sen munapussien tuottoon ja elossasäilymiseen siten, että 8-10 vrk infektion jälkeen huomattavasti pienempi osa loisituista kuin loisettomista naaraista kantoi munapusseja ja noin kolme viikkoa infektion jälkeen loisittujen yksilöiden kuolleisuus lisääntyi loisettomiin verrattuna. Altistuksella sinänsä ei ollut vaikutusta munapussien tuottoon ja elossasäilymiseen. Tulokset poikkeavat aiemmin Kanadassa toisella hankajalkaislajilla tehtyjen kokeiden tuloksista ja saattavat johtua eroista loisten määrissä, kokeen kestossa ja hankajalkaisten ruokinnasta tai ruokailukyvystä kokeiden aikana.

Siian lihaksissa esiintyvä plerokerkoiditoukka on pitkäikäinen, joten loisia kertyy kaloihin niiden iän mukana. Myös loisten vuosittainen kertymisnopeus näytti kasvavan vanhemmissa kaloissa yhdellä tutkimusalueista, jossa yli 5-vuotiailla kaloilla esiintyi yleisesti yli 20 loista kalaa kohti. Muutos kertymisnopeudessa ei liittynyt esim. muutoksiin siikojen kasvussa tai sukukypsyyden saavuttamiseen. Lisäksi ilmiö oli nähtävissä saman ikäisissä kaloissa kolmena vuotena peräkkäin, joten se ei voinut aiheutua voimakkaasta loisinvaasiosta yhtenä tai useampana edeltävänä vuonna. Mahdollisesti siiat alkavat kerätä lisää loisia, kun loismäärä niissä ylittää tietyn kynnyksen, joka kuitenkin vaihtelee yksilöittäin. Tämä voisi johtua esimerkiksi immuunipuolustuksen heikkenemisestä suuren loismäärän vuoksi, tai siitä, että suuri loistaakka lisää siikojen ravinnon tarvetta ja saa ne syömään enemmän, vaikka lisääntynyt ravinnonotto ei näykään kalojen kasvussa. Takautuvasti lasketut ikäkohtaiset pituudet ja korrelaatiot kalojen pituuden tai painon ja loisten määrän välillä antoivat samansuuntaisia viitteitä loisinnan ja kasvun välisestä yhteydestä: nuorissa kaloissa loisia on eniten suurilla yksilöillä, kun taas vanhoissa kaloissa loisia on eniten pienillä yksilöillä. Tällainen tilanne voisi johtua siitä, että suuremmat kalat syövät enemmän planktonia kuin pienemmät ja altistuvat suuremmalle määrälle loisia, joka heikentää vanhemmiten niiden kasvua. Todisteita loisen aiheuttamasta kuolleisuudesta ei löydetty. Haukimadon vaikutus siikojen kasvuun näyttää keskittyneen vanhoihin kaloihin, joihin myös suurin osa loisista on kertynyt.

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Original papers

I

The use of parasites as tags to elucidate differences between whitefish populations

by

Katja Pulkkinen and E. Tellervo Valtonen

Archiv für Hydrobiologie Special Issues Advances in Limnology 1998 50: 257-271.

II

The influence of food competition and host specificity on
the circulation pattern of parasites through coregonid hosts

by

Katja Pulkkinen, E. Tellervo Valtonen, Asko Niemi and
Kauko Poikola

Manuscript (submitted)

III

Accumulation of plerocercoids of *Triaenophorus crassus*
Forel (Cestoda) in the second intermediate host *Coregonus
lavaretus* and their effect on growth and mortality of the
host

by

Katja Pulkkinen and E. T. Valtonen

IV

Effect of *Triaenophorus crassus* (Cestoda) infection on the
behavior and susceptibility to predation of the first
intermediate host *Cyclops strenuus* (Copepoda)

by

Katja Pulkkinen, Anna F. Pasternak, Tiina Hasu and E.
Tellervo Valtonen

Manuscript (submitted)

V

Factors affecting abundance of *Triaenophorus* infection in *Cyclops strenuus*, and parasite-induced changes in host fitness

by

Anna F. Pasternak, Katja Pulkkinen,Viktor Mikheev, Tiina Hasu and E. Tellervo Valtonen