Exploitation of *Anodonta piscinalis* (Bivalvia) by trematodes: parasite tactics and host longevity

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In a long-lived molluscan host, trematode adaptations that minimize the risk of parasite-induced host mortality may evolve because the residual reproductive value of a parasite would not be limited by a short life-span of the host. Two features of the host exploitation (site selection and timing of the reproductive period) were examined for the bucephalid trematodes *Rhipidocotyle fennica* and *R. campanula* in their first intermediate host *Anodonta piscinalis* which is a long-lived freshwater clam. The gonad, assumed to be less critical for survival of the host, was the organ most frequently parasitized by both of the parasite species. Except for the kidney in the case of *R. campanula*, the prevalence of infection was low in organs that were expected to be important for host survival (kidney, gills, digestive gland). We also made a literature survey on the site selection of larval trematodes of aquatic molluscs in general. We found that the longer the life-span of the host, the higher the proportion of trematode-mollusc associations where the gonad is the main site of infection. Infected *A. piscinalis* do not reproduce due to parasitic castration but the uninfected individuals develop their offspring, presumably, during the period of most abundant resources in the seasonally fluctuating environment. Therefore, if the parasites adjust their cercarial production to the same period as the uninfected clams they should minimize mortality caused by an energetic stress for the host. We found the reproductive period of *R. fennica* to co-occur with that of the host, while the cercarial production of *R. campanula* started 2 weeks earlier than the host reproduction. In summary, *R. fennica* followed a "damage avoidance tactic" but *R. campanula* to a lesser extent.

1. Introduction

Intramolluscan stages, sporocysts or rediae, of digenean trematodes reproduce asexually producing enormous numbers of cercarial larvae. The intensive production of cercariae is usually accompanied by excessive damage to, or even death of, the host (e.g. Ginetsinskaya 1988).

Two opposing views have developed concerning the importance of host survival for intramolluscan

stages of trematodes. Firstly, it has been thought that a well-adapted parasite will not kill its host. The opposite opinion is that survival of the host mollusc is not important to trematodes — as soon as the armada of cercariae is released into the environment, ensuring completion and maintenance of the parasite life cycle, the host individual is no longer needed (Lauckner 1986).

Whether the survival of the host individual is important to an intramolluscan stage of a trematode parasite may depend on the longevity of the host, since it contributes to the residual reproductive value (Williams 1966a) of the parasite. Stearns (1992) defined the residual reproductive value, RRV, as the number of offspring that an average organism in a particular age class can expect to have after the current reproductive event. For a trematode which infects a short-lived mollusc, the RRV is low. In this case, taking as much resources as possible from the host for its own reproduction, whatever the influence on host survival, could be expected to be a parasite tactic that would be selected for. On the other hand, it may be hypothesized that the RRV of a parasite in a long-lived host can be high since additional reproductive periods of the parasite in the future are not limited by a short life-span of the host. Under these circumstances, a parasite tactic which tends to minimize the risk of host mortality, may evolve.

The aim of this study was to examine two aspects of the host exploitation tactics of the bucephalid trematodes *Rhipidocotyle fennica* and *R. campanula*, namely site selection and timing of the reproductive period, in a long-lived freshwater bivalve, *Anodonta piscinalis*. Since *A. piscinalis* is a long-lived mollusc, the parasites should prefer to (1) penetrate organs which are of low importance for survival of the host, and (2) reproduce during a period when resources available for the host are most abundant.

According to Lauckner (1983), bivalves can not get rid of bucephalid trematodes once infected. This is supported by the finding of Haaparanta and Valtonen (1991) that *A. piscinalis* has practically no defensive ability against *R. fennica*. Furthermore, infections with *R. fennica* or *R. campanula* have been found to increase mortality of *A. piscinalis* in the laboratory (Taskinen & Jokela 1995). Thus, in our study system there were two parasites which were capable of increasing host mortality, and the hosts could not expel the parasites from their body.

2. Materials and methods

Anodonta piscinalis Nilss. (Mollusca, Bivalvia, Unionidae) (= *A. anatina* L.) is a common and abundant dioecious freshwater clam in northern Europe. It matures at the age of 2–4 years and reproduces annually reaching a maximum age of 15–20 years and a maximum length of 100–120 mm (Økland 1963, Negus 1966). In Finland, female *A. piscinalis* develop glochidia-larvae during July and August in their outer gill blades (Jokela *et al.* 1991, Pekkarinen 1993). The glochidia over-winter in the gills to be released next spring (Økland 1963, Negus 1966, Jokela *et al.* 1991, Pekkarinen 1993). Before the beginning of benthic life, the glochidia are ectoparasitic on fish for about four weeks, and can infect several fish species (Jokela *et al.* 1991).

Digenean trematodes of the family Bucephalidae are parasites of bivalves and fish (e.g. Lauckner 1983). Bucephalid species *Rhipidocotyle fennica* and *R. campanula* use *Anodonta piscinalis* and the cyprinid fish *Rutilus rutilus* as their first and second intermediate hosts, respectively. The final host for *R. fennica* is the esocid fish *Esox lucius* and for *R. campanula* the percid fish *Perca fluviatilis* (Taskinen *et al.* 1991, Gibson *et al.* 1992). Taskinen *et al.* (1994) found profound seasonal changes in the occurrence of the developmental stages of both *Rhipidocotyle* species in *A. piscinalis*, but no clear seasonality in the prevalences of infection. *Rhipidocotyle* infection decreases the fecundity of *A. piscinalis* and is age-, size-, sex- and habitat-specific, being absent in immature clams and more common among large specimens, females and those collected from the littoral zone than in small individuals, males or sublittoral clams (Taskinen & Valtonen 1995).

A total of 1 157 *Anodonta piscinalis* in 43 samples were collected using a bottom dredge between May 1987 and November 1989 from Lake Saravesi, central Finland (62°25´N, 26°00´E) and 1 486 clams in 31 samples between April and October 1989 from Lake Kuivasjärvi, northern Finland (65°00´N, 25°30´E). Lake Saravesi is small (7.8 km²), shallow (mean depth 5.5 m), eutrophic and ice-covered on average from late November until early May. The highest water temperatures are reached at the end of July or beginning of August. Lake Kuivasjärvi is even smaller and shallower (0.84 km², mean depth 1.9 m). It is a hypereutrophic lake which has a 2-km outlet to the Baltic Sea, and is covered by ice from late October until early May. Maximum water temperatures occur in July. There is a very dense *A. piscinalis* population in the littoral zone of Lake Kuivasjärvi. In Lake Saravesi, clams were found both from the littoral and the sublittoral zones. Water temperatures were measured daily during the ice-free period. For sampling dates, procedures, water temperatures and descriptions of the study sites, see Taskinen *et al.* (1994).

The clams were dissected and the occurrence of egg cells and/or glochidia-larvae of the clams was observed visually from the outer gill blades. During 1989 the reproductive status of clams was not checked in Lake Saravesi. In May 1987 and November 1989, the gonad, digestive gland, kidney region, mantle, gill blades and foot of 144 clams (both males and females) from Lake Saravesi were separated and pressed

piece by piece between two large glass plates and examined for trematodes using transmitted light and $120 \times$ magnification. In the case of Lake Kuivasjärvi, all the organs, except for the gills, were examined for trematodes, and the reproductive status of clams was documented for all the 1 486 clams.

Age of the clams was determined from the growth rings on the shell (Haukioja & Hakala 1978a). For monitoring cercarial emergence, 10–15 clams ≥ 4 years of age from each sample were, immediately after sampling, placed separately in a 5-litre aquarium filled with tap-water with aeration and kept at room temperature in the laboratory. The clams were monitored during the sampling day and the following day, between 8 and 10 am for *R. fennica* and from 2 to 4 pm for *R. campanula*, because they have a different period of the most prolific cercarial emergence (Taskinen *et al*. 1991).

Furthermore, a literature survey on localization of larval trematodes in aquatic molluscs was also made. The number of papers checked was 177, twenty-two of which contained the desired information (cf. Table 4).

χ^2-test was used to analyse differences in the prevalence of *Rhipidocotyle* infection between various organs of *A. piscinalis*, and in the proportion of host–parasite associations where the gonad was the main site of infection when short-lived and long-lived hosts were compared.

3. Results

3.1. Site selection of the parasites

For both *Rhipidocotyle* species the sporocysts (sporocyst = the intramolluscan stage in the life cycle of the trematode family Bucephalidae) were long and branching tubules. Prevalences of *R. fennica* infection in various organs of *A. piscinalis* differed significantly from each other in Lake Saravesi ($\chi^2 = 111.62$, $df = 6$, $p < 0.001$). In 92% of the clams infected with *R. fennica*, the parasite was found in the gonad. Second highest prevalence was observed in the mantle which was occupied in 87% of the parasitized clams (Table 1). All infected clams had either the gonad or mantle parasitized. Quite high prevalences were detected in the kidney region and around the digestive gland which were invaded in 79% and 64% of the infected clams, respectively. Lower prevalences occurred in the actual digestive gland tissue (36%), gills (18%), and foot (7%) (Table 1).

There was also a difference in the relative quantity of *R. fennica* sporocyst tubules between the organs of *A. piscinalis* (Table 1). The amount of sporocyst material was frequently high in the gonad, kidney region and around the digestive gland. However, inside the actual tissue of the gland the quantity of sporocyst tubules was never high, being only one or two short tubules in each case. The sporocyst "network" in the mantle was generally sparse and in only a few cases was it dense or widely distributed. In the gills and foot, only single tubules were encountered (Table 1).

The sporocyst tubules of *R. fennica* in the mantle were usually situated in the posterior part, close to the siphons of the host. In the gills, the tubules were always located near the base of the gills, and in the foot they were close to the gonad. The sporocyst tubules found in the foot were always in poor condition and without any cercarial production. In other

Table 1. Prevalences (%) of *Rhipidocotyle fennica* and *R. campanula* in various organs of *Anodonta piscinalis*. DG1 = tissues in digestive gland surrounding the actual gland tissue, DG2 = actual gland tissue in the digestive gland, Inf. = number of clams infected, P1 = prevalence of infection, P2 = prevalence of infection when only the parasitized clams were included, Q = relative quantity of sporocyst tubules.

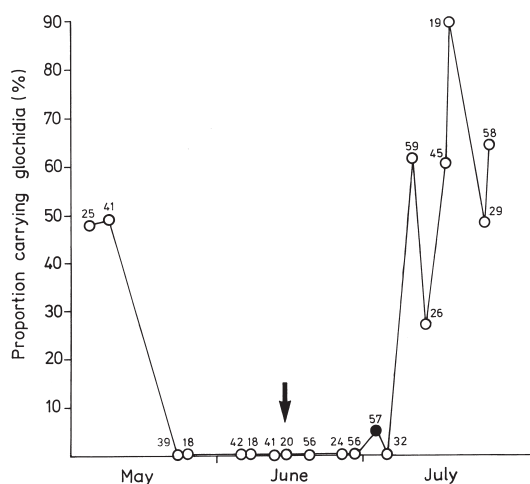| | *R. fennica* (n = 144) Lake Saravesi 1987–89 | | | | *R. campanula* (n = 1 468) Lake Kuivasjärvi 1989 | | | |
	Inf.	P1	P2	Q	Inf.	P1	P2	Q
Gonad	36	25	92	High	85	6	100	High
Mantle	34	24	87	Low	31	2	36	Low
Kidney	31	22	79	High	84	6	99	High
DG1	25	17	64	High				
DG2	14	10	36	Low	14	1	16	Low
Gills	7	5	18	Low				
Foot	3	2	7	Low	0	0	0	Zero
Combined	39	27			85	6		

Fig. 1. Proportions of uninfected, mature (≥ 4 years) *Anodonta piscinalis* carrying glochidia in each sample taken from Lake Kuivasjärvi during May–July 1989. The numbers of clams studied are indicated in the figure. The start of *Rhipidocotyle campanula* cercarial emergence is indicated by arrow, and the beginning of *A. piscinalis* glochidial development is shown with a black dot.
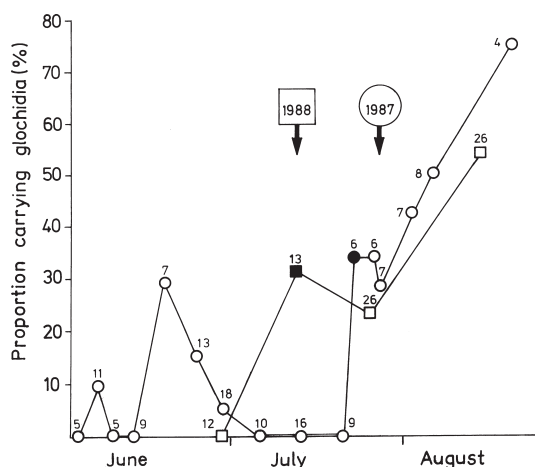

Fig. 2. Proportions of uninfected, mature (≥ 4 years) *Anodonta piscinalis* carrying glochidia in each sample taken from Lake Saravesi during June–August 1987 (circles) and 1988 (squares). The numbers of clams studied are indicated in the figure. The start of *Rhipidocotyle fennica* cercarial emergence is indicated by an arrow, and the beginning of *A. piscinalis* glochidial development is shown with a black dot (1987) or square (1988).

tissues, cercarial development at least to germ ball stage (Woodhead 1929) took place.

Differences in the prevalence of *Rhipidocotyle campanula* between various organs of *Anodonta piscinalis* in Lake Kuivasjärvi were also significant (Yates corrected $\chi^2 = 287.70, df = 4, p < 0.001$). Every infected clam had sporocyst tubules in the gonad and 99% had them in the kidney region. In all the other tissues the prevalence of infection was low: 36% and 16% of the parasitized clams had sporocyst tubules in the mantle and in the digestive gland tissue, respectively. Sporocysts of *R. campanula* were never found in the foot (Table 1).

The quantity of *R. campanula* sporocyst tubules in various organs, and the distribution of sporocyst tubules within an organ, followed a similar pattern to that of *R. fennica*. The relative quantity of *R. campanula* sporocyst tubules was high in the gonad and kidney area. In the mantle and in the digestive gland tissue the quantity was low (Table 1). Furthermore, cercarial development at least to the germ ball stage was observed in all infected organs.

3.2. Reproductive cycle of the host

Female clams released over-wintered glochidia-lar-

vae and started the production of new glochidia earlier in the more northerly situated Lake Kuivasjärvi when compared with Lake Saravesi. In Lake Kuivasjärvi, all the clams released glochidia between 9 and 22 May (Fig. 1). No glochidia were detected in the gills in June. In Lake Saravesi, the clams released over-wintered glochidia later, but also during a longer period than in Lake Kuivasjärvi. During 1987 some clams carried over-wintered glochidia even at the end of June, although the proportion of glochidia-bearing clams had already decreased in May.

Development of *A. piscinalis* glochidia took place earlier in Lake Kuivasjärvi than in Lake Saravesi. In Lake Saravesi 1987, development started with the transportation of new egg cells into the gills between 22 and 24 July (Fig. 2, Table 2). The development of *A. piscinalis* glochidia takes about four weeks (Jokela *et al.* 1991). Thus, since all females could be considered to carry new glochidia between early August and mid-August (Fig. 2), the glochidia could be estimated to be fully developed by mid-September (Table 2). During 1988, the developmental period of glochidia could be estimated to range from mid-July to mid-September (Table 2). In Lake Kuivasjärvi, the development of glochidia started already between 28 June and 3 July, and continued till mid-August (Table 2).

Water temperatures at the beginning and end of *A. piscinalis* glochidial development, as well as sum of day-degrees from the 1st of May to the start of the reproductive period, are given in Table 2. In Lake Kuivasjärvi, the glochidia production of clams started at a lower temperature and with a lower sum of day degrees, and ceased at a higher temperature than in Lake Saravesi (Table 2).

3.3. Reproductive period of the parasite

Production of cercariae of *R. campanula* started between 12 and 14 June, and ceased between 15 and 21 August in Lake Kuivasjärvi (Table 3). That of *R. fennica* began between 28 and 30 July, and stopped between 21 September and 2 October in Lake Saravesi in 1987. The average dates of the first and last observation of emerged *R. fennica* cercariae during 1987–89 were 21 July and 17 September, respectively (Table 3).

Cercarial production of *R. campanula* in Lake Kuivasjärvi also started at a lower temperature (16.8°C), and ceased at a higher temperature (18.0°C) — the average temperatures on the date of the beginning and end of that of *R. fennica* in Lake Saravesi were 20.3°C and 11.6°C, respectively (Table 3). In addition, the sum of day-degrees (°D) from the 1st of May to the first observation of cercarial emergence was clearly lower for Lake Kuivasjärvi (515) than for Lake Saravesi (mean 1 105, range 1 030–1 260). The difference in the duration of cercarial emergence between the lakes was not remarkable (Table 3) (see also Taskinen *et al*. 1994).

4. Discussion

4.1. Parasite site selection

Organs of *Anodonta piscinalis* can be assumed to vary in their importance for the survival of the clam.

Table 2. Developmental period of *Anodonta piscinalis* glochidia. No eggs = the latest date when eggs had not been transported into the gills, Start = beginning of the glochidial development (the date of the first observation of eggs in the gills), End = termination of the glochidial development, S = Lake Saravesi, K = Lake Kuivasjärvi, T1 and T3 = water temperatures (°C) at the beginning and at the end of glochidial development, respectively. T2 = sum of day-degrees from the beginning of May to the beginning of glochidial development.

	No eggs	Start	T1[a)	T2 [a)	End [b)	T3[(a
1987 S	22 July	24 July	21	916	Mid-September	11–12
1988 S	29 June	13 July	24	1 030	Mid-September	12–14
1989 K	28 June	3 July	19	869	Mid-August	17–19

[a) Temperatures were measured at the depth of one meter below the surface.
[b) Since the development of *A. piscinalis* glochidia takes about four weeks (Jokela *et al*. 1991), the termination date of the glochidial development period is given as the date when all females in the population were considered to carry eggs, embryos or glochidia plus four weeks.

Table 3. Period of parasite cercarial emergence. The dates of the first and last observations of emergence are given in the colums "Start Yes" and "End No", respectively. The latest date when the emergence had not yet begun, and the first date when it already had ceased, are given in the columns "Start No" and "End Yes", respectively. S = Lake Saravesi, K = Lake Kuivasjärvi, F = *Rhipidocotyle fennica*, C = *R. campanula*. T1 and T3 are water temperatures (°C) at the first and last observation of emergence, respectively. T2 = sum of day degrees from the beginning of May to the first observation of emergence, D = duration of the emergence (days) from the first to the last observation of emerging cercariae.

	Start No	Start Yes	T1	T2	End No	T3	End Yes	D
1987 S, F	28 July	30 July	19.0	1 030	21 Sep.	10.4	2 Oct.	55
1988 S, F	29 June	13 July	24.0	1 030	21 Sep.	11.0	8 Oct.	72
1989 S, F	4 July	20 July	18.0	1 260	8 Sep.	13.4	11 Nov.	51
Mean S, F	21 July		20.3	1 105	17 Sep.	11.6		59
1989 K, C	12 June	14 June	16.8	515	15 Aug.	18.0	21 Aug.	63

Such organs as the gills, digestive gland and kidney region including the heart, are important to vital functions. On the other hand, we assumed damage to the gonad to be less harmful to the host since Rotschild (1941) found no signs of increased mortality in molluscs with the gonad removed artificially by X-rays. As expected, the gonad was most frequently and intensively invaded by both *Rhipidocotyle* species. The prevalence and quantity of sporocyst tubules in the gills and digestive gland were low. In the kidney region the amount of sporocyst tubules was always high when infected. Also the prevalence of infection in the kidney region was high for both parasites but especially for *R. campanula* (99%, $n = 85$, and 79%, $n = 39$, among the infected individuals for *R. campanula* and *R. fennica*, respectively; Yates corrected $\chi^2 = 12.34$, $df = 1$, $p < 0.001$). The higher prevalence in kidney may contribute to the higher mortality of laboratory-kept *A. piscinalis* parasitized by *R. campanula* when compared with those infected with *R. fennica* reported by Taskinen and Jokela (1995).

Fat and glycogen content of uninfected female *Anodonta piscinalis* is markedly higher in the gonad than in the mantle, gills, foot or the rest of the soft tissues (Jokela *et al.* 1993). So, by locating themselves in the gonad, the parasites may combine low risk of host mortality with availability of abundant energy.

4.2. Reproductive period of the host and the parasites

The reproductive period of *R. fennica* coincided with the development of the clam offspring in Lake Saravesi. In Lake Kuivasjärvi, the reproductive period of *R. campanula* ended simultaneously, but started about 2 weeks earlier than that of the host. The observed timing of parasite reproduction could be an adaptation to: (1) limit the risk of host mortality, or (2) enhance transmission to fish. The latter is unlikely since potential second intermediate hosts for both *Rhipidocotyle* species, cyprinid fishes, as well as final hosts, are present throughout the year. Furthermore, the densities of fishes in the littoral zone of the lakes are highest in May during the spawning period of the fish, not during the period of maximum parasite cercarial release.

As stated by Lack (1966), organisms generally time the most energy-consuming phases of their

annual cycle with periods when resources are abundant. Although the infected clams usually are castrated, the period of glochidial development of uninfected clams is the period of the most abundant resources also for the parasitized specimens. The parasite cercarial production probably is highly energy demanding, since *Rhipidocotyle fennica* produces on average 9 500 cercariae per day (Taskinen *et al.* 1991) depleting almost completely the glycogen reserves of *A. piscinalis* (Jokela *et al.* 1993). Thus, we propose that by adjusting their reproduction to the period when resources for the host are at a high level the parasites are able to increase their energy and nutrient intake in a way that increases the risk of host mortality as little as possible.

The coincidence of host and parasite reproductive periods could also be a direct effect of increased host resources during early summer fuelling increased parasite reproductive activity or, simply, an independent response of the parasite, controlled by water temperatures. However, the between-year differences in the temperatures and sums of day degrees at the first observation of cercarial emergence of *R. fennica* and, particularly, the great difference in the water temperature at the beginning of *R. campanula* cercarial emission between the present study (16.8°C) and that found by Ivantsiv and Chernogorenko (1984) for the same species (22–24°C) suggest that the observed timing of *Rhipidocotyle* reproduction is not merely due to similar temperature dependent developmental processes of the host and parasite.

4.3. Parasite host-exploitation tactic: adaptation to a long-lived host?

Host exploitation of *Rhipidocotyle fennica*, in terms of site selection and timing of reproductive period, could be characterized as a "damage avoidance tactic", one which combines low costs (mortality) with high benefits (energy). It seemed that *Rhipidocotyle fennica* avoided the costs more than *R. campanula*. The present results are in accordance with the finding of Jokela *et al.* (1993) that during its reproduction, *R. fennica* uses that part of the energy reserves of *Anodonta piscinalis* which are allocated to reproduction, rather than those allocated to maintenance of the host (glycogen and fat, respectively).

The sporocysts of bucephalid trematodes survive up to the death of their host clam (Lauckner 1983).

For such a parasite, the kind of behaviour found in the present study could be selected for if the host is long-lived, since in such a host as *A. piscinalis*, with a maximum life span of 15–20 years, the residual reproductive value (Williams 1966a) of the parasite is high when compared with a mollusc with a life-span of only 1–2 years.

Redia and sporocyst stages, which parasitize

Table 4. Localization of larval trematodes in aquatic molluscs of different life-spans. Ga = Gastropoda, B = Bivalvia, R = redia, S = sporocyst, D = digestive gland, G = gonad, K = kidney, V = base of the visceral spire.

Host	Parasite	Main site	
Life-span 1–2 years			
Helisoma corpuletum, Ga	*Petasiger chandleri*, R	D	(1)
H. trivolvis, Ga	*Glypthelmins pennsylvaniensis*, S	D	(2)
H. anceps, Ga	*Echinostoma trivolvis*, R	D	(3)
H. anceps, Ga	*Petasiges nitidus*, R	D	(3)
H. anceps, Ga	*Halipegus occidualis*, R	D	(3)
H. anceps, Ga	*Haematoloechus longiplexus*, S	D	(3)
H. anceps, Ga	*Plagitura parva*, S	D	(3)
H. anceps, Ga	*Diplostomulum schreuringi*, S	D	(3)
H. anceps, Ga	*Megalodiscus temperatus*, R	D	(3)
H. anceps, Ga	Spirorchid sp., S	D	(3)
Lymnaea peregra, Ga	*Diplostomum gasterostei*, S	D	(4)
L. truncatula, Ga	*Fasciola hepatica*, R	D	(5)
L. glabra, Ga	*F. hepatica*, R	D	(6)
L. tomentosa, Ga	*F. hepatica*, S	D	(7)
L. truncatula, Ga	*F. hepatica*, R	D	(8)
Galba truncatula, Ga	*F. hepatica*, S	D	(7)
Biomphalaria spp., Ga	*Schistosoma* spp., S	D	(9)
Life-span 3–4 years			
Littorina littorea, Ga	*Cryptocotyle lingua*, R	D, G	(10)
L. littorea, Ga	*Himasthla leptosoma*, R	D, G	(10)
L. littorea, Ga	*Renicola roscovita*, S	V	(10)
Nassarius obsoletus, Ga	*Zoogonus rubellus*, S	G	(11)
Life-span > 4 years			
Patella vulgata, Ga	*Cercaria patella*, R	D	(12)
Ilyanassa obsoleta, Ga	*Australobilharzia variglandis*	G	(13)
I. obsoleta, Ga	*Himsthla quissetensis*, R	G	(13)
I. obsoleta, Ga	*Lepocreadium setiferoides*	G	(13)
I. obsoleta, Ga	*Zoogonus* sp., S	G	(13)
Buccinium undulatum, Ga	*Cercaria buccini*, S	D	(14)
B. undulatum, Ga	*Zoogonoides viviparus*, S	D, G	(15)
Elliptio dilatata, B	*Rhipidocotyle papillosum*, S	G	(16)
Lampsilis siliquoidea, B	*Rhipidocotyle septpapillata*, S	G	(17)
Dreissena polymorpha, B	*Bucephalus polymorphus*, S	D	(18)
D. polymorpha, B	*B. polymorphus*, S	D	(19)
Anodonta piscinalis, B	Bucephalidae sp., S	G	(20)
A. piscinalis, B	*Rhipidocotyle campanula*, S	G	(21)
Unio pictorum, B	*R. campanula*, S	G	(21)
Marine bivalves, B	Bucephalidae spp., S	G	(22)
A. piscinalis, B	*R. campanula*, S	G, K	(23)
A. piscinalis, B	*R. fennica*, S	G	(23)

(1) Abdel-Malek 1962, (2) Cheng and Cooperman 1964, (3) Fernandez and Esch 1991, (4) Williams 1966, (5) Southgate 1970, (6) Rondelaud *et al.* 1987, (7) Humiczewska and Taracha 1987, (8) Hourdin *et al.* 1992, (9) Basch 1991, (10) Robson and Williams 1971, (11) Cheng *et al.* 1973, (12) Rees 1934, (13) Curtis and Hurd 1983, (14) Køie 1971, (15) Køie 1987, (16) Woodhead 1929, (17) Kniskern 1952, (18) Kinkelin *et al.* 1968, (19) Baturo 1977, (20) Haukioja and Hakala 1978b, (21) Chernogorenko and Ivantsiv 1980, (22) Lauckner 1983, (23) The present study.

molluscs, have a special role in the life cycle of digenean trematodes. They produce enormous numbers of cercariae which emerge and infect the second intermediate host or the definitive host. Natural selection should maximize the trematode's total lifetime reproductive output, or in a mollusc, the total life-time number of cercariae produced. That is the product of the number of reproductive seasons and the number of cercariae produced per reproductive season. For a trematode, there should be a trade-off between the number of cercariae produced per reproductive season and the number of reproductive seasons, since the resource allocation hypothesis by Williams (1966b) and Charnov and Krebs (1973) assumes that reproduction of an organism decreases the probability of its survival. By locating themselves in the gonad of the host rather than in some vitally important organ, and by producing cercariae during the period when resources for the host are abundant, *Rhipidocotyle* species, at least *R. fennica*, may partially break this trade-off. In a short-lived mollusc, this trade-off may be insignificant because the short life-span of the host limits the number of reproductive seasons of a trematode.

Support for this hypothesis was found in the literature on localization of larval trematodes in aquatic molluscs (Table 4). The proportion of host–parasite associations where the main site of infection was the gonad was zero in short-lived hosts (1–2 yrs, $n = 17$) but increased to 50 and 71% in hosts of 3–4 ($n = 4$) and > 4 yrs ($n = 17$) life-span, respectively. The difference was statistically significant (1–2 yrs vs. long-lived: Yates corrected $\chi^2 = 15.38$, $df = 1$, $p < 0.001$). A similar pattern was found when only the gastropods were included. Within gastropods the proportions of host–parasite associations with the gonad as the main site of infection were zero ($n = 17$), 50 ($n = 4$) and 57% ($n = 7$) in age-groups 1–2, 3–4 and > 4 yrs, respectively (1–2 yrs vs. long-lived: Yates corrected $\chi^2 = 8.51$, $df = 1$, $p < 0.01$).

The longer the life-span of the host the greater may be the relative importance of the number of reproductive seasons for the total life-time reproductive output of the intramolluscan stages of a trematode. Consequently, the selective pressure favouring any behaviour of a trematode that minimizes parasite-induced host mortality should be stronger in a long-lived molluscan host than in a short-lived one.

Essential to this "damage avoidance hypothesis" is that the parasites can reproduce many times in a same host. Mayerhof and Rotschild (1940) kept long-lived gastropod in the laboratory for several years: *Littorina littorae* lived five years, giving off *Cryptocotyle lingua* cercariae throughout that period!

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