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Effect of the castrating trematode parasite *Rhipidocotyle fennica* on energy allocation of fresh-water clam *Anodonta piscinalis*

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Summary

1. If host survival is important to a parasite, it should avoid the use of the host's maintenance energy. Selective use of the host's energy is possible by selecting which part of the host to penetrate and when to be active.

2. We study the effects of the castrating trematode parasite *Rhipidocotyle fennica* on energetics of fresh-water clam *Anodonta piscinalis*.

3. Before production of offspring, uninfected clams allocate energy to shell growth and glycogen storage. During offspring production shell growth slows down, clams lose weight and consume the stored glycogen. Concurrently the fat content of clams increases indicating the collection of long-term storage for maintenance during the winter.

4. Infected clams lack glycogen reserves and are lighter, but contain more fat than uninfected clams. Parasite reproduction occurs concurrently with the development of offspring in uninfected clams. During their reproduction, parasites use the energy that would otherwise be directed to host reproduction, without interfering with the maintenance energy of the host. Using only the reproductive energy is an efficient way to use the host without causing increased risk of mortality.

Key-words: Energy storage, host reproduction, parasitism, Trematoda, Unionidae

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Introduction

Parasites use hosts for transportation and for supply of energy (Price 1980; Holmes 1983). According to the allocation principle (Cody 1966), assimilated energy is allocated to reproduction, growth and maintenance. Obviously, energy that a parasite appropriates, affects some or all of these functions in the host. A successful 'parasite strategy' is one where the host is not killed before it has fulfilled its function from the parasite point of view (Anderson & May 1982; Read & Schrag 1991). Therefore, parasites are facing a classical optimization problem: how to utilize the host efficiently without killing it before its function is fulfilled?

One option is that the parasite uses the energy allocated by the host to growth and reproduction and does not interfere with the host's maintenance energy. This tactic may evolve by natural selection, especially if the hosts are long-lived, iteroparous organisms and can be used as hosts for a long period of time.

The options for a set of tactics to use the host's energy are partly determined by the allocation pattern of the host. For example, in 'capital' breeders (Sibly & Calow 1984; Stearns 1989) energy is allocated to reproduction via some storage while in 'income' breeders energy is allocated to reproduction directly after assimilation. Furthermore, allocation to reproduction often follows some temporal, e.g. seasonal, pattern. Therefore, parasites can use host energy selectively by location and timing of their activity in the host.

Trematodes commonly cause infertility in their molluscan hosts (Lauckner 1983). For example, in the fresh-water clam, *Anodonta piscinalis* Nills. (Mollusca, Unionidae) (= *Anodonta anatina* L.), the gonad tissue may be replaced by branching parasite sporocysts (Taskinen 1992). In molluscs the proportion of assimilated energy allocated to reproduction is relatively high (Bayne, Salkeld & Worrall 1983; Mackie 1984; Sprung 1991) and, as suggested by Taskinen (1992), by penetrating into the gonad and synchronizing the production of cercariae with offspring production in uninfected *Anodonta*, trematodes can efficiently use the host's reproductive energy. However, in the bulk of literature on trematode–mollusc

interactions, studies of energy allocation and parasitism are rare.

We studied the energetic effects of *Rhipidicotyle fennica* Gibson, Taskinen, Valtonen, 1992 (Trematoda, Bucephalidae) infection on *Anodonta*, focusing on (1) how *A. piscinalis* allocates energy to reproduction, directly or using storage, and (2) how *Rhipidocotyle* infection affects the somatic condition and energy allocation pattern of the host clams.

Study system

LIFE CYCLE OF *ANODONTA PISCINALIS*

Anodonta piscinalis is a common and abundant freshwater clam in northern Europe. It matures at 2–4 years of age and reproduces annually reaching maximum life span of >15 years (Ökland 1963; Negus 1966; Haukioja & Hakala 1978a). From the beginning of July to mid-August glochidia larvae are developed in the outer gill blades of the females (Jokela, Valtonen & Lappalainen 1991) where they are stored (Ökland 1963; Negus 1966) and maintained (Richard, Dietz & Silverman 1991) over winter to be released next spring (Ökland 1963; Negus 1966; Haukioja & Hakala 1978a). The larvae are ectoparasites on several common fish, e.g. roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) (Jokela *et al.* 1991).

LIFE CYCLE OF *RHIPIDOCOTYLE FENNICA*

Rhipidocotyle fennica uses *A. piscinalis* as the first intermediate host (Taskinen, Valtonen & Gibson 1991). Branching sporocyst tubules of *R. fennica* invade mainly the gonad of a clam and produce cercariae (Taskinen 1992). Prevalence of infection is usually below 25% (J. Jokela & J. Taskinen, unpublished observations). Female clams suffer higher prevalence of infection than males (Taskinen 1992). The cercariae emerge from the clams between late July and September (Taskinen 1992). At the late stage of infection gonad tissue is almost entirely replaced by the parasite sporocysts and clams are unable to reproduce (Taskinen 1992). Before castration, clams may reproduce once or twice (Taskinen 1992). The second intermediate host of *Rhipidocotyle fennica* is roach and the life cycle is completed in pike (*Esox lucius* L.).

Materials and methods

Reproductive and heavily parasitized female clams were collected from four sites in central Finland. The first sample was collected in late July (22–24 July), just before cercarial emergence (Taskinen *et al.* 1991). At this time the development of fertilized eggs to glochidia is just about to start (Jokela *et al.* 1991). The second sample was collected in mid-October (19–20 October), when glochidia were fully developed and cercarial emergence was finished.

The clams at sites chosen for this study can be considered to represent distinct populations. Although all sites belong to the same water system, they are separated by lake basins and clam dispersal among them is unlikely. The study sites differ in bottom quality, depth and resource level (Table 1). Clams also have different growth rates at different sites (Table 1). Sites are subjected to roughly the same regional temperatures and seasonal rhythm. Clam populations in all sites have high prevalence of *Rhipidocotyle fennica* infection (J. Taskinen, unpublished observation).

At both sampling dates a scuba diver collected about 200 clams from each site. They were transported live to the laboratory. The first five reproductive and the first five heavily infected females that were between 5 and 8 years of age and between 60 and 85 mm in length (Table 1) were chosen as a sample. The sex and state of parasitism were determined by pressing a piece of gonad between glass plates under a dissection microscope (Taskinen *et al.* 1991). Length of the year rings and total length of the clam were measured with Vernier calipers (Haukioja & Hakala 1978b) to calculate growth during the season.

The foot, mantle, gill blades, gonad and rest of the visceral mass (= 'body') of each clam were separated to indexed plastic cups and dried at 60 °C for 48 h. Dry mass was measured to 0·1 mg, fat content as a proportion of mass lost during the diethylene–ether extraction (Reznik 1983) and glycogen content by using amyloglucosidase from *A. niger* (no. 102857, Boehringer Mannheim, Mannheim, Germany) for hydrolysis of glycogen and an UV photometric kit for glucose assay (no. 263826, Boehringer Mannheim).

Differences in the growth of the clams were analysed with three-way analysis of variance. Growth was calculated by subtracting the length of the last year ring from total length. Population (four study

Table 1. Bottom quality and productivity of the habitat and length (in mm, mean ± SD), age [in years, median (min–max)], length at the third annulus (in mm, mean ± SD) and number of clams collected at each site

	Bottom material	Productivity	Length	Age	Length at third annulus	*n*	Depth (m)
Site 1	Sand	Oligotrophic	68·1 ± 4·90	7 (6–8)	37·4 ± 3·38	20	5–6
Site 2	Sand	Mesotrophic	77·0 ± 3·76	7 (6–8)	46·5 ± 6·90	21	5–6
Site 3	Clay/sand	Mesotrophic	78·1 ± 3·81	6·5 (5–8)	50·1 ± 5·04	20	1–3
Site 4	Mud/clay	Eutrophic	75·8 ± 2·59	6 (5–7)	52·3 ± 6·74	20	1–2

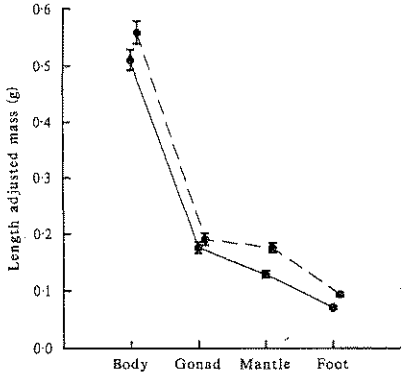

Fig. 1. Length-adjusted dry mass (back transformed mean ± SE) of different parts of the clam in relation to state of parasite infection: uninfected clams (----); infected clams (——).

sites), date of sampling (July, October) and state of infection (yes, no) were used as class variables in the model.

Because length is correlated with dry mass in clams (Haukioja & Hakala 1978a), it was used as a covariate in the analysis of dry masses. A MANCOVA model where body, gonad, mantle and foot masses were used as response variables and state of infection (INF), date of sampling (TIME) and population (POPU) as factorial variables was used. The mass of gills, where the developing glochidia are located, was excluded from the analysis to enable changes mediated by developing glochidia in the clam to be followed. The assumptions of homogenous slopes (Wilkinson 1990) and normally distributed, homoscedastic residuals were fulfilled after logarithmic (i.e. natural logarithms—ln) transformation of dry masses of different parts of the clam.

Fat and glycogen content of body, gonad, mantle, foot and gills were used as response variables in two MANOVA models built to analyse the differences in respect to state of infection, time of observation and study site. Glycogen contents were ln-transformed to achieve normally distributed residuals. Assumption of homogenous variances was univariately checked using Cochran's test (Day & Quinn 1989).

All statistical analyses were performed with SYSTAT statistical package (Wilkinson 1990).

Results

A total of 81 clams was examined (Table 1). A complete record of fat and glycogen content of all parts was available for 72 and 49 clams respectively.

DRY MASS

The mass of the body (including hepatopancreas, adductor muscles, etc.) accounted for the largest proportion (55·6%) of the mass of the clam if gills are excluded. Gonad and mantle accounted for roughly equal proportions, 19·4% and 16·0%, respectively, and foot 8·4% of the total dry mass. Mass of offspring produced was on average 19% of the total dry mass of the clam.

Multivariate results of MANCOVA suggest significant differences in the dry masses in respect to all main effects, infection (INF), time (TIME) and population (POPU) (Table 2). Additionally, interaction between TIME and POPU is statistically significant.

Infected clams were generally lighter than uninfected ones (Fig. 1). Univariate statistics (effect INF) suggest that this is due to decreased mass of the mantle and foot (Table 2, Fig. 1).

Both infected and uninfected clams lost weight between July and October (Fig. 2). Decrease in the dry mass is statistically significant in all parts except in the body (Table 2, Fig. 2). Differences in the length-adjusted dry masses among populations show no clear trend but are statistically significant for the foot and body (Table 2).

Univariate analysis suggests that statistical significance of the multivariate interaction term TIME*POPU is due to differences in the mass of foot (Table 2). At site 1 the mean length-adjusted dry mass of the foot decreased between July (0·099 g) and October (0·071 g), at sites 2 and 4 it did not change and at site 3 it increased (from 0·065 g in July to 0·075 g in October).

Table 2. Multivariate (Wilks Λ) and univariate *F*-statistics of multivariate analysis of covariance of the dry mass of clams. Ln-transformed length of the clam as a covariate

	Wilks Λ		Body		Gonad		Mantle		Foot	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Infection (INF)	8·03	< 0·001	3·02	NS	1·03	NS	19·92	< 0·001	19·41	< 0·001
Time (TIME)	6·48	< 0·001	1·20	NS	14·48	< 0·001	22·65	< 0·001	2·21	< 0·001
Population (POPU)	2·68	0·003	3·28	0·026	2·18	NS	0·35	NS	5·75	0·002
INF*TIME	1·12	0·355	0·03	NS	3·23	NS	2·14	NS	0·91	NS
INF*POPU	0·97	0·480	1·09	NS	2·29	NS	1·64	NS	1·76	NS
TIME*POPU	2·68	0·003	1·56	NS	2·61	NS	0·92	NS	3·61	0·018
INF*TIME*POPU	0·32	0·985	0·22	NS	0·35	NS	0·21	NS	0·21	NS
LN LENGTH	4·50	0·003	17·86	< 0·001	9·13	0·004	5·65	0·020	5·42	0·023

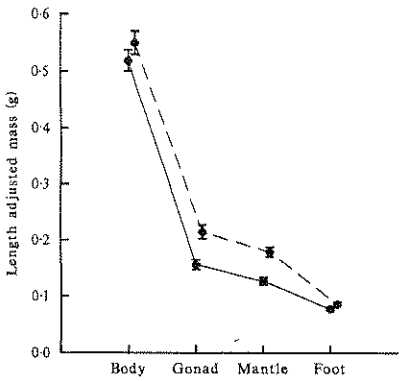

Fig. 2. Length-adjusted dry mass (back transformed mean ± SE) of different parts of the clam in relation to time of sampling: July (----); October (——).

FAT CONTENT

Of the parts studied, gonad and body had highest fat content (Figs. 3 and 4). In the infected clams the proportion of fat in the gonad was especially high (16·6%) (Fig. 3).

Highly significant multivariate main effects suggest that fat contents of clams differed between infected and uninfected individuals (INF), between July and October (TIME) and among populations (POPU) (Table 3). Infected clams had significantly more fat in gonad, mantle and foot (Fig. 3, Table 3). Clams sampled in October had a significantly higher proportion of fat in mantle, foot and gills but less in the gonad than clams sampled in July (Fig. 4, Table 3).

Differences in the fat content among populations are not as consistent. The statistical significance of the multivariate interaction is due to differences among populations in the fat content of body, mantle and foot (Table 3).

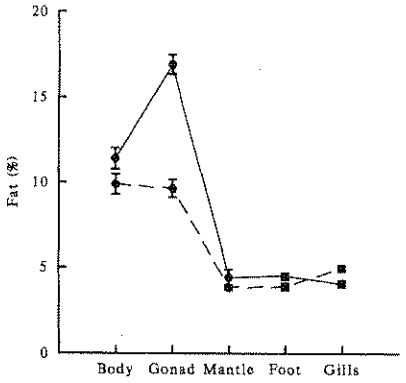

Fig. 3. Fat content (%) of the different parts of the clam in relation to state of parasite infection: uninfected clams (----); infected clams (——).

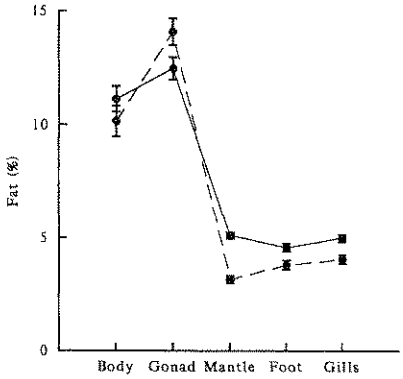

Fig. 4. Fat content (%) of the different parts of the clam in relation to time of sampling: July (----); October (——).

The statistically significant multivariate interaction INF*TIME indicates that the fat content of infected and uninfected individuals changes in different directions during the study period. Univariate analysis reveals that changes take place in gonad and gills (Table 3). The fat content of the gonads of infected individuals was higher in July (18·6 ± 4·0%, mean ± SD) than in October (15·2 ± 3·6%) while that of uninfected individuals was slightly lower in July (9·5 ± 2·7%) than in October (9·7 ± 2·7%). On the other hand, the fat content of the gills of infected individuals rose to the level of uninfected ones in October (from 3·1 ± 1·1% in July to 5·0 ± 0·8% in October) when in uninfected individuals no change occurred (4·8 ± 1·5% in July and 5·0 ± 0·8% in October). Univariate analysis suggests that the interaction TIME*POPU is statistically significant only because mantle fat content of the

Table 3. Multivariate (Wilks Λ) and univariate *F*-statistics of multivariate analysis of variance of fat content of clams

	Wilks Λ		Body		Gonad		Mantle		Foot		Gills	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Infection (INF)	21·09	< 0·001	3·06	NS	90·25	< 0·001	7·39	0·009	4·70	0·035	11·83	0·001
Time (TIME)	15·67	< 0·001	1·23	NS	4·46	0·039	82·56	< 0·001	8·10	0·006	13·45	0·001
Population (POPU)	3·45	< 0·001	3·36	0·025	2·29	NS	6·67	0·001	3·16	0·001	1·80	NS
INF*TIME	4·22	0·003	2·34	NS	5·27	0·025	0·03	NS	1·05	NS	12·90	0·001
INF*POPU	0·96	0·501	0·15	NS	0·88	NS	1·43	NS	2·70	0·054	0·02	NS
TIME*POPU	1·83	0·035	0·23	NS	2·17	NS	4·61	0·006	1·02	NS	0·49	NS
INF*TIME*POPU	0·85	0·624	0·31	NS	1·02	NS	0·52	NS	0·96	NS	1·90	NS

Table 4. Multivariate (Wilks Λ) and univariate *F*-statistics of multivariate analysis of variance of the glycogen content of clams

	Wilks Λ		Body		Gonad		Mantle		Foot		Gills	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Infection (INF)	9·19	< 0·001	17·56	< 0·001	49·40	< 0·001	11·65	0·002	2·37	NS	3·04	NS
Time (TIME)	1·57	0·200	0·12	NS	0·91	NS	0·16	NS	4·71	0·037	0·86	NS
Population (POPU)	1·84	0·043	1·38	NS	5·23	0·005	0·04	NS	1·57	NS	1·11	NS
INF*TIME	1·49	0·223	4·68	0·038	6·94	0·013	1·90	NS	0·38	NS	0·04	NS
INF*POPU	1·22	0·277	0·58	NS	1·64	NS	1·21	NS	1·14	NS	0·34	NS
TIME*POPU	1·30	0·223	1·80	NS	0·82	NS	0·52	NS	2·06	NS	0·78	NS
INF*TIME*POPU	1·28	0·235	0·48	NS	3·65	0·022	0·42	NS	1·26	NS	0·73	NS

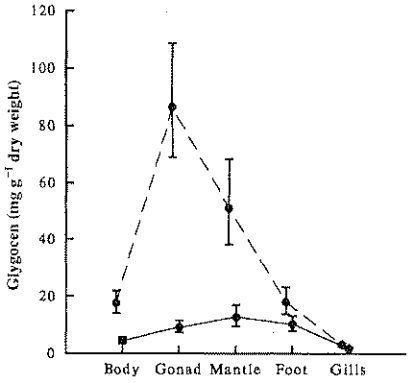

Fig. 5. Glycogen content (back transformed mean ± SE) of different parts of the clam in relation to state of parasite infection: uninfected clams (----); infected clams (——).

clams of different populations changes in opposite directions between sampling dates (Table 3). However, detailed analysis reveals that in all study sites fat content of the mantle almost doubles from July to October except in site 4 where this increase is smaller (from 2·8 ± 1·1%, 2·1 ± 1·2%, 3·1 ± 0·6% and 4·6 ± 0·5% in July to 5·3 ± 1·1, 4·9 ± 1·1%, 5·0 ± 0·8% and 5·2 ± 0·9% in October in sites 1, 2, 3 and 4 respectively).

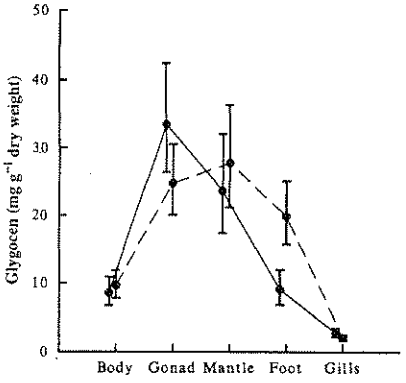

Fig. 6. Glycogen content (back transformed mean ± SE) of different parts of the clam in relation to time of sampling: July (----); October (——).

GLYCOGEN CONTENT

Infected clams contained clearly less glycogen than uninfected ones (Fig. 5, Table 4). Univariate analysis indicates statistically significant differences in the glycogen content of body, gonad and mantle (Table 4) between infected and uninfected individuals. Glycogen content was eight times higher in the gonads of uninfected than in infected individuals (Fig. 5). Differences in the glycogen content among populations were also statistically significant (Table 4). When univariate statistics are included, general differences among populations are reduced to differences in the glycogen content of the gonad. In univariate analysis the interaction effect INF*TIME also is statistically significant for gonad and body (Table 4). In both cases infected clams gained (from 12·3 and 4·4 mg g^{-1} in July to 16·08 and 5·7 mg g^{-1} in October for gonad and body respectively) and uninfected lost glycogen between sampling dates (from 116·5 and 20·6 mg g^{-1} in July to 63·9 and 12·6 mg g^{-1} in October for gonad and body respectively) (Fig. 6).

SHELL GROWTH OF THE CLAMS

The growing season of the clams is considered to start in May when the water warms up (Taskinen 1992). Clams grew more in the first half of the growing season than in the second (Table 5). No differences in growth were detected among populations (ANOVA, $F_{3,63} = 1·78$, $P = 0·159$), between infected and uninfected (ANOVA, $F_{1,63} = 0·53$, $P = 0·470$) and between

Table 5. Growth of the clams (mm) during the season (mean ± SE). Growth has been assumed to start at May when water temperature rises. 'Additional growth' corresponds to growth after July relative to growth in the whole season. It is calculated by subtracting mean growth at July from mean growth at October and dividing this by mean growth at October

	May–July	May–October	Additional growth (%)
Uninfected	6·52 ± 0·448	7·38 ± 0·537	11·7
Infected	6·32 ± 0·405	6·95 ± 0·573	9·1

sampling dates (ANOVA, $F_{1,63} = 1{\cdot}44$, $P = 0{\cdot}234$). The non-significant TIME effect indicates that growth after July is not large enough to be discernible from the growth before July.

Discussion

REPRODUCTIVE CLAMS

Female clams lose weight and glycogen during the reproductive period. This suggests that clams use glycogen stored in the body and gonad for production of glochidia. Offspring production must require a lot of energy because the mass of offspring corresponds to 19% of the total mass of a clam. Lighter gonad, mantle and foot (Fig. 2) in females after offspring production is an indication of reproductive stress. At the same time fat content of the gonad and especially the mantle increases. Doubling the fat content of the mantle from July to October may indicate allocation to long-term energy storage for maintenance during the winter and so, obviously, energy assimilated between July and October is allocated not only to reproduction but also to storage.

This scenario does not include shell growth. Shell growth is an important component of clam fitness because the possible number of offspring produced is a function of size (Haukioja & Hakala 1978a). Female clams grow primarily before glochidia production starts (Table 5) and thus growth provides more room for developing glochidia.

The seasonal allocation pattern thus corresponds to models of optimal energy allocation developed by Kozłowski and Uchmański (1987) and Kozłowski (1991).

Among population differences in the dry mass, fat content and glycogen content indicate differences in condition. However, the pattern of energy allocation during reproduction is the same in all populations. Significant multivariate interactions between TIME and POPU in the analysis of dry masses and fat content are only due to an increase in foot dry mass in site 3 and the high fat content of the mantle in site 4 in July.

INFECTED CLAMS

Heavy trematode infection has profound effects on the energetics of *Anodonta*. Parasitized females are lighter than healthy reproductive ones (Fig. 1). The difference is due to the decreased mass of mantle and foot in infected females. The mass of the gonad of the infected individuals reflects more the mass of the parasite tissue itself and therefore does not decrease when parasites invade the gonad. On the other hand, the body contains the organs that are important for the maintenance of the clam and reduction in these would possibly decrease the survival of the host.

The most profound effects of parasites are on the glycogen content of the clams. Infected clams contain substantially less glycogen than uninfected ones (Fig. 5). The difference is so large that parasites can be said to deplete the glycogen storage. This has also been reported for trematode infection in bivalves (Lauckner 1983) and gastropods (Becker 1980). In July, parasite cercariae in infected clams were already developed and ready to be released while in uninfected clams the development of glochidia in the gill blades was just about to start. Parasites may thus have already depleted the glycogen reserves of clams in July and used them to produce cercariae.

Surprisingly, infected females had a higher fat content than uninfected ones (Fig. 3). This is mainly due to very high proportions of fat in the gonads of infected females (Fig. 3). Because most of the tissue in the gonads consists of trematode sporocysts an obvious conclusion is that trematode sporocyst must contain a lot of fat. Cercariae are known to swim actively after release and may use lipids as an energy base (Taskinen *et al.* 1991).

PARASITIC INTRUSION TO ALLOCATION SYSTEM

Our results show that *Rhipidocotyle fennica* can use the energy allocation system of *Anodonta* selectively and utilize the energy that a clam normally allocates to its own reproduction. Penetration into the gonad and timing of cercariae production makes selective use of host energy possible (Taskinen 1992). We suggest that in infected clams assimilated energy is processed as normal, part is directed to maintenance and perhaps growth, but energy allocated to developing eggs and glochidia is redirected to production of cercariae. Overall, our results support the suggestion of Taskinen (1992) that parasites practise a 'sparing' tactic minimizing the decrease in host survival due to infection. The possible negative effect of trematode infection on population dynamics of the host is dampened, because prevalence of infection is moderate, spatially variable and infected clams may reproduce once or twice before the castration occurs (Taskinen 1992).

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