Digenean parasites of the bivalve mollusc *Pisidium amnicum* in a small river in eastern Finland

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ABSTRACT: The host-parasite relationship between digeneans and a semelparous population of the mollusc *Pisidium amnicum* Müller in a small river in eastern Finland was studied during 1992/1993. The parasite prevalence of the population was high. The total prevalence was 45.6% in 1992 (n = 790) and 47.5% in 1993 (n = 160). The dominant digenean, *Bunodera luciopercae* (34.2% in 1992, 35.0% in 1993), had highest prevalences in July/August and in winter. Two other species, *Palaeorchis crassus* (7.8% in 1992, 7.5% in 1993) and *Phyllodistomum elongatum* (4.7% and 5.0%), were rare during the winter. The prevalence of *B. luciopercae* increased as clams aged, while the other species were most common in middle-sized clams. Apparently *B. luciopercae* rediae dominate over *P. elongatum*, which has only sporocyst stages, while *P. crassus*, which has large rediae, is more deleterious to the clam and induces host mortality. Double infections were significantly less common (1.2%) than might be expected by chance. All parasites castrated their hosts; no clam containing both parasites and embryos was found. Semelparity of the population is apparently caused by parasitic castration.

KEY WORDS: Digenea · Clam · Castration · *Pisidium amnicum* · *Bunodera luciopercae* · *Palaeorchis crassus* · *Phyllodistomum elongatum* · River · Seasonality

INTRODUCTION

The freshwater bivalve mollusc *Pisidium amnicum* (O.F. Müller, 1774) is the largest species in the genus *Pisidium* with a shell length of up to 10 mm. It lives in slow-running, shallow streams and in lakes near estuaries (Boycott 1936). *P. amnicum* lives in the sediment and feeds on the bacteria from interstitial water (Lopez & Holopainen 1987). Its life-span is 1 to 3 yr. These bivalves are hermaphroditic with facultative autogamy and ovoviviparity, and both semelparous (only 1 reproductive cycle during a lifetime) and iteroparous (several reproductive cycles) populations exist (Holopainen & Hanski 1986).

The presence of digeneans in *Pisidium amnicum* was noted by Brown (1927), Wesenberg-Lund (1934), Danneel & Hinz (1976), Holopainen & Hanski (1986), and Holopainen & Penttinen (1993). The physiology and ecology of *P. amnicum* in a southern Finnish popula-

tion was studied by Holopainen & Ranta (1977a, b) and Holopainen (1979). They noted that the population was infected with larval digeneans; however, the parasites were not studied in detail. Digenean parasites of *P. amnicum* have been studied in detail only by Zhokhov (1987, 1991a, b). He examined trematodes of 11 *P. amnicum* populations from tributaries of the Volga River (Zhokhov 1991b). The most common species found was *Bunodera luciopercae* (Müller) in all populations, but *Palaeorchis* sp. and *Phyllodistomum elongatum* Nybelin were also present. He also found *Phyllodistomum pseudofolium* Nybelin, *Crepidostomum* sp., *Allocreadium isoporum* Looss and *Diplostomum* sp. (Zhokhov 1991b). The focal population of the present study in eastern Finland was part of a previous ecological study on the effects of parasites on host life history (see Holopainen et al. 1997).

In the life cycle of *Bunodera luciopercae* the first intermediate hosts are species of the genera *Pisidium* and *Sphaerium* (Wisniewski 1958) and many cladocerans and copepods may serve as the second intermediate hosts. The definitive hosts are perch *Perca flu-*

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viatilis and ruffe *Gymnocephalus cernuus*. The most important definitive host of *B. luciopercae* in Finland is perch (Rahkonen et al. 1984). In Canada, Cannon (1972) examined 14 fish species for *B. luciopercae* when prevalence was high in molluscs; yellow perch (*Perca flavescens*) was the only host. Pojmanska (1984) found *B. luciopercae* in perch and zander (*Stizostedion lucioperca*) in Poland. *Bunodera luciopercae* has a biennial life history: during the first winter it parasitizes the first and second intermediate hosts and subsequently it infects fish definitive hosts (Andrews & Chubb 1980, Rahkonen et al. 1984).

Phyllodistomum spp. are parasites of the urinary system of fishes. They do not have a redial stage like *Bunodera luciopercae*; only cercariae develop in sporocysts. In additional to *Pisidium* spp., *Sphaerium* species can also serve as the first intermediate host of *Phyllodistomum elongatum* (Zhokhov 1987). The body of the metacercaria encysts in the anterior part of the cercarial tail, and the released metacercaria is preyed upon directly by the definitive host (Rahkonen & Valtonen 1987). Zhokhov (1991a) found 2 types of cercariae in *Pisidium amnicum*. The smaller cercariae are poorer swimmers and have a shorter life-span than the larger type. Smaller ones may also encyst in molluscs (Zhokhov 1991a). Both smaller cercariae and larger encysted metacercariae emerge from clams; small cercariae infect fry and young fish while adult fish become infected by the metacercariae (Zhokhov 1987). According to Zhokhov (1987), the crucian carp *Carassius carassius* is the definitive host of *P. elongatum*.

The genus *Palaeorchis* and its life cycle are very poorly known. The worm develops in rediae and has a tailless, non-emerging cercariaeum. Species of the genus *Palaeorchis* differ from the related genus *Asymphylodora* by having only 1 testis. For a description of *Palaeorchis crassus* stages in the clam of the present study see Niewiadomska & Valtonen (1998).

The purpose of this study was to describe the parasite communities and their dynamics in 1 *Pisidium amnicum* population in eastern Finland over a 2 yr period and to elucidate the host-parasite relationships according to seasonal variation and host size, and also to investigate the influence of digeneans on the intermediate hosts. The significance of digeneans on the population dynamics of *P. amnicum* is discussed by Holopainen et al. (1997).

MATERIALS AND METHODS

The study area in eastern Finland (62° 37' N, 29° 45' E) is a small, slowly running (0.1 to 0.5 m³ s⁻¹), shallow river with a mud bottom. At the estuary its width is 3

to 4 m and its depth 1.5 to 2.0 m. The stream is ice-covered from November/December to April. Clams normally exist to depths of 1.2 m.

A total of 950 *Pisidium amnicum* specimens was collected by hand-net (mesh size of 0.5 mm) in 22 successive samplings between May 1992 and November 1993. Sample size averaged 43 clams (range 10 to 83; see Figs. 1 & 2). Clams under 4 mm were not collected routinely, but in June 1994 an additional sample of ca 100 clams of all size classes was taken.

The emergence of cercariae was examined by keeping the clams in the sample water in a petri dish at room temperature (18 to 20°C) for 24 h after collection.

Clams were weighed, their length measured and after removal of the shells soft tissues were squashed between 2 glass plates and examined for parasites. The fresh weight of the soft tissues was obtained by subtracting shell weight from total weight. Gravidity of clams was determined by looking for embryos in marsupia. Digeneans were identified using both living cercariae in water with a drop of methyl cellulose and cercariae relaxed by warming. Prevalence of infection and developmental stage of parasites (sporocysts, rediae, cercariae) were noted.

The association of digenean species in single clams was determined by comparing whether the presence of double infections in pair-wise comparisons were more or less common than expected by chance. The statistical significance of these associations and the monthly variations in prevalence were determined using the independence test with likelihood ratio statistics G (Sokal & Rohlf 1981). Risk level alfa was 0.05.

RESULTS

The total prevalence of digenean infections in *Pisidium amnicum* was 45.6 % in 1992 (n = 790) and 47.5 % in 1993 (n = 160) (Fig. 1). The most abundant species was *Bunodera luciopercae*, which had a prevalence of 34.2 % in 1992 and 35.0 % in 1993. A smaller number of clams were infected by *Palaeorchis crassus* (7.8 % and 7.5 %) and *Phyllodistomum elongatum* (4.7 % and 5.0 %) in 1992 and 1993, respectively.

Only 1.2 % of the clams had concurrent infection of 2 digenean species (Table 1). There was a negative association in all pair-wise comparisons (Table 1), which was statistically significant only in the case of *Bunodera luciopercae* and *Palaeorchis crassus*.

Considerable seasonal variation occurred in the prevalence of *Bunodera luciopercae* (Fig. 1). The species existed in the clams throughout the study period. In 1992, when more samples and greater sample sizes were collected, highest *B. luciopercae* prevalences were found in July/August and in winter. Some *Palae-*
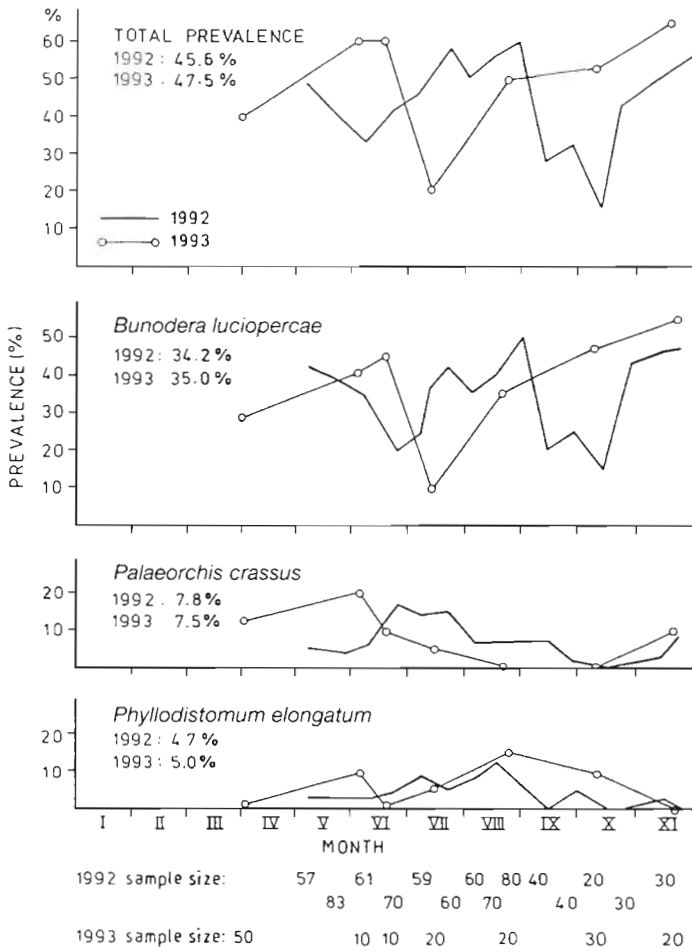
Fig. 1. *Pisidium amnicum.* Seasonal variation of trematode parasites in clams during 1992 and 1993
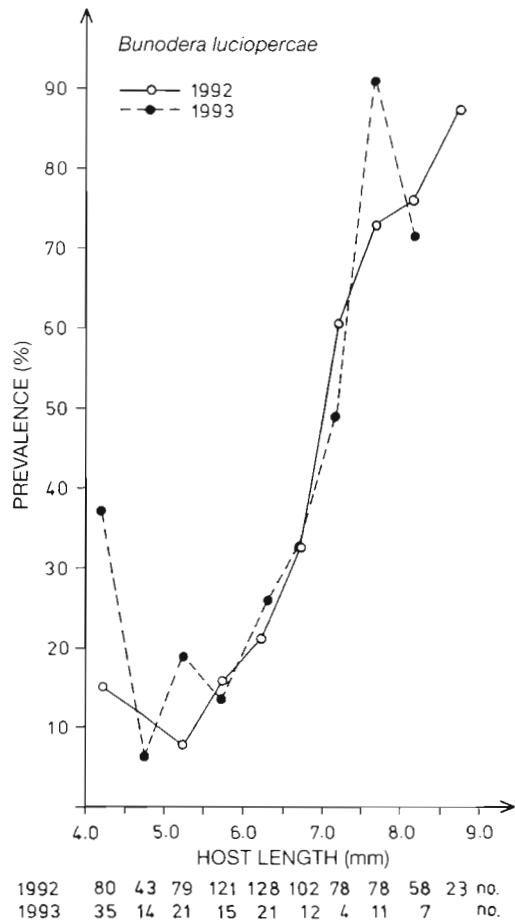

Fig. 2. Prevalence of *Bunodera luciopercae* in clams *Pisidium amnicum* in relation to host length during the years 1992 and 1993. No. = number of clams

orchis crassus-infected clams were present throughout the study, but this species had a clear infection peak in May/June in both years. *P. crassus* was least abundant in September/October; prevalence increased again in November. *Phyllodistomum elongatum* was found in the clams by early spring, although the infection peak was in August and the species disappeared in November in both years.

The prevalences of *Bunodera luciopercae* increased with increasing shell length of the host (Fig. 2), which

Table 1. Concurrent digenean infections in clams *Pisidium amnicum* in eastern Finland in 1992/1993. Total no. of clams = 950. Bun: *Bunodera luciopercae*; Pal: *Palaeorchis crassus*; Phy: *Phyllodistomum elongatum*

Infection	No. clams	Prevalence	Pearson's χ^2	p
Bun + Pal	1	0.1%	−0.140	<0.001
Bun + Phy	9	0.9%	−0.056	0.270
Pal + Phy	2	0.2%	−0.029	1.000

was also seen when separate samples were studied relative to class size (Fig. 3). Hosts over 9 mm in length were all parasitized. *Palaeorchis crassus* (Figs. 3 & 4) and *Phyllodistomum elongatum* (Figs. 3 & 5) were most abundant in middle-sized clams (length 6 to 8 mm). The prevalences of all species were lowest in the smallest size classes. However, clams under 3 mm in length (n = 26) collected in 1994 had no parasites. The relationship between the size of the host and parasite prevalence was significant for all species (G^2-test; p < 0.001 in all cases).

The emergence of cercariae was studied in 1992. Cercariae of *Bunodera luciopercae* emerged over a 2 mo period between July 21 and September 28. The cercariae of *Phyllodistomum elongatum* emerged during a shorter period from August 3 to August 31. *Palaeorchis crassus* does not have free-swimming cercariae.

The most profound observed effect of digeneans on the host was castration. All species castrated their hosts. Clams containing both parasites and embryos were never found.
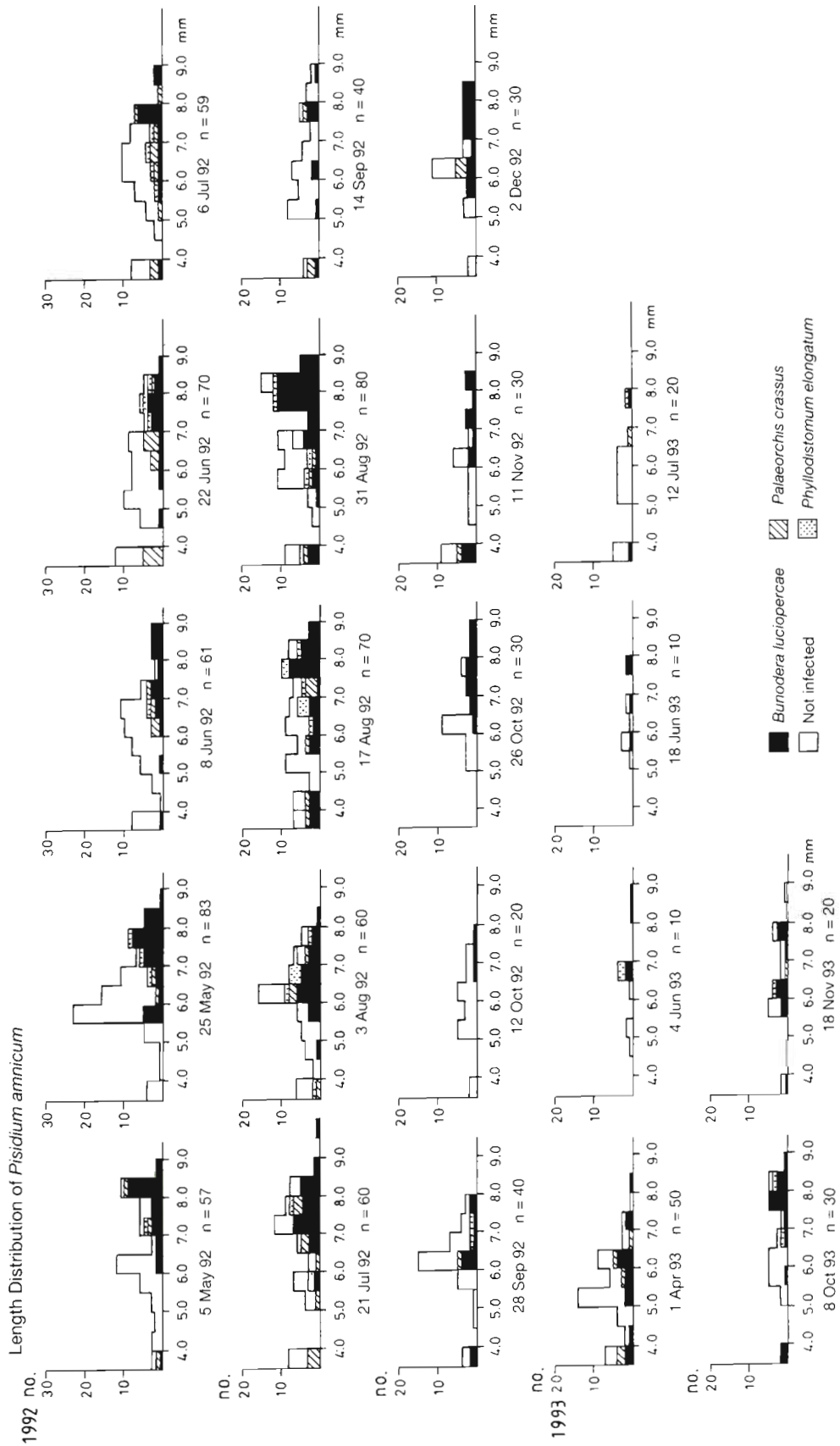
Fig. 3. *Pisidium amnicum*. Length (mm) distribution of samples and proportions of clams infected with 3 digenean species during 1992 and 1993. Sample from August 1993 (n = 20) is not included
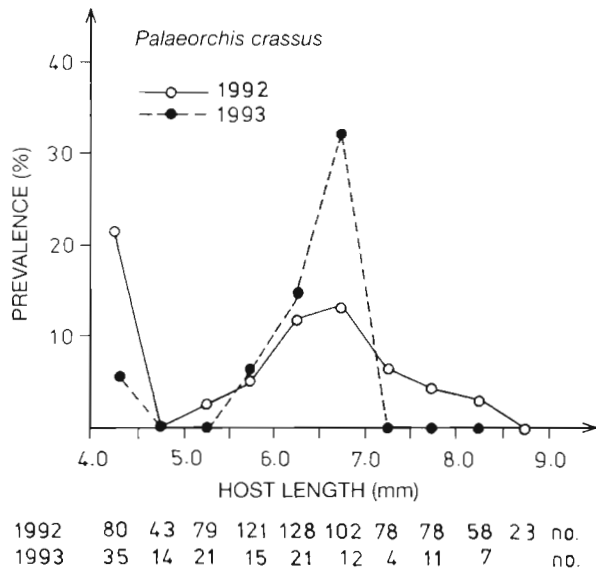
Fig. 4. Prevalence of *Palaeorchis crassus* in clams *Pisidium amnicum* in relation to host length during 1992 and 1993

Palaeorchis crassus infection significantly increased the weight of the soft tissues of the host in relation to the total mass (G^2-test p = 0.007). *Bunodera luciopercae* had the opposite effect (G^2-test, p < 0.001). *P. crassus* appeared to have the most serious effect on the host. Most *P. crassus*-infected clams had heavy infections (>100 cercariae in a clam), causing the loss of most host tissues. Thus the increase in weight of soft tissues was due to increase in parasite mass. Also, the shells were brittle and easily damaged. Only a few clams with light infections were found.
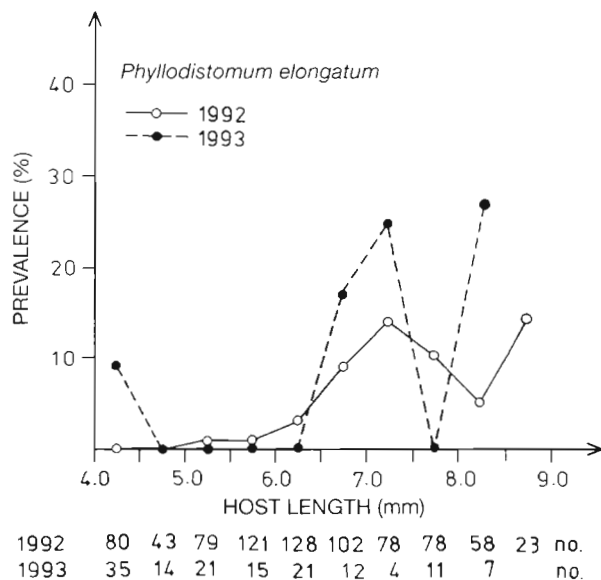

Fig. 5. Prevalence of *Phyllodistomum elongatum* in clams *Pisidium amnicum* in relation to host length during 1992 and 1993

DISCUSSION

The 3 species (*Bunodera luciopercae*, *Palaeorchis crassus* and *Phyllodistomum elongatum*) found herein are the same as those observed in the Volga River basin by Zhokhov (1991b), where *B. luciopercae* was the most common species and *P. elongatum* and *Palaeorchis* sp. were relatively rare. Zhokhov (1991b) also found *Crepidostomum* sp., *Allocreadium isoporum*, *Phyllodistomum pseudofolium* and *Diplostomum* sp. from *Pisidium amnicum*, but he studied several clam populations, which probably increased the number of species found.

The prevalence of *Bunodera luciopercae* in the present material increased rapidly with increasing size of the host, while the 2 other species (*Palaeorchis crassus* and *Phyllodistomum elongatum*) were more prevalent in middle-sized clams. Increasing prevalence with increasing host size is common in mollusc-digenean associations (see Lauckner 1983). Taskinen & Valtonen (1995) noted a similar distribution among *Rhipidocotyle fennica*-infected *Anodonta piscinalis*.

The different patterns in size-associated prevalences of *Phyllodistomum elongatum* and *Palaeorchis crassus* compared to *Bunodera luciopercae* might be explained by parasite-induced host mortality. Indeed, *P. crassus* probably causes mortality of its clam host; tissues of *P. crassus*-infected clams were almost totally replaced by rediae in most cases. Shells were brittle and easily fragmented.

The life cycle of the ovoviviparous *Pisidium amnicum* and its relation with *Bunodera luciopercae* is as follows: young clams are born in June/July; sexual maturation and subsequent fertilization occur the next July/August at the age of 13 mo. Parturition is after 11 mo gravidity the next June/July. Gravid clams are infected by *B. luciopercae* miracidia in early summer at age ca 24 mo. Fertilization (or growth of young at least) of the potential second brood of the infected mollusc host is prevented by developing sporocysts and rediae (host castration). *B. luciopercae* cercariae are liberated from *P. amnicum* after ca 14 mo the next August/September, when most clams die at the age of ca 38 mo (see also Holopainen et al. 1997). Cercariae infect the second intermediate host, Cyclopoida or Cladocera species, which are eaten by the definitive host, usually perch. The ingested metacercariae mature during winter in the intestine of the fish and gravid worms are lost by early summer from the perch intestine (Cannon 1971, Rahkonen et al. 1984).

According to Lauckner (1986), survival of naturally short-lived hosts is not important for digeneans because, after reproduction, hosts will die soon even without parasites. Consequently digenean parasites of *Pisidium amnicum* might be expected to be more

harmful to their short-living hosts in comparison with clams with a longer life-span. In long-lived hosts, i.e. *Anodonta piscinalis*, which can live 14 yr in Finland, bucephalid digeneans *Rhipidocotyle fennica* continue to live and produce cercariae for years until the host dies. There are indications that *R. fennica* infections do not induce host mortality (Jokela et al. 1993, Taskinen et al. 1997). We, however, suggest that the dominant parasite of *P. amnicum*, *Bunodera luciopercae*, is not very pathogenic to its clam host because its prevalence increases with increasing length of the clam.

Species having rediae can replace species having sporocysts only (Fernandez & Esch 1991a, b, Sousa 1992, 1993). This is explained by the mobility and digestive system of rediae, which can consume sporocysts of the other species (Lie 1973). *Bunodera luciopercae* rediae might dominate over *Phyllodistomum elongatum*, which has only sporocyst stages and this might explain some of the increase of *B. luciopercae* in older clams. However, *Palaeorchis crassus* has larger rediae than *B. luciopercae*, but its prevalence decreases in older clams.

Zhokhov (1991b) noted that concurrent digenean infections in *Pisidium amnicum* were rare but increased slightly with age. In his work less than 0.5% of 1 yr old clams harboured more than 1 digenean species, the prevalences of double infections for 2 and 3 yr old clams being 1.4 and 2.4%, respectively. The dominance of 1 species is more common among short-lived host species (Crews & Esch 1986), whereas concurrent infections are suggested to be more common in long-lived host species, because they have more time to acquire different parasites (Zhokhov 1991b). However, this was not found in central Finland: only 1 joint infection by *Rhipidocotyle fennica* and *R. campanula* was found in 1157 long-living *Anodonta piscinalis* clams (Taskinen at al. 1991), while 12 joint infections were found in short-living *Pisidium amnicum* clams examined in this study. Fernandez & Esch (1991a, b) as well found only 7 double digenean infections in 4899 *Helisoma anceps* snails in North Carolina.

The relative rarity of *Palaeorchis crassus* and *Phyllodistomum elongatum* may also be caused by the shortage of other host species in their life cycles. There may also be other reasons, external to the host, affecting the structure of the trematode community. For example, Williams & Esch (1991) observed that the most common parasite species were influenced by the type of vegetation and substratum present. Host population dynamics also affect the dynamics of trematode infections by increasing the temporal heterogeneity of digenean species (Fernandez & Esch 1991a).

A seasonal cycle was noted for both *Palaeorchis crassus* and *Phyllodistomum elongatum* during both years studied, with infection peaks in the summer and an autumnal decrease. In 1992 highest *Bunodera luciopercae* prevalence values were noted in July/August, when a new *B. luciopercae* generation was seen in young clams. A sharp decrease was noted in early September, when the majority of cercariae had been released from clams and the exhausted old clams died. The differences in the *B. luciopercae* seasonal cycle in 1993 as compared to 1992 might be due to fewer samples and the smaller number of clams collected in 1993.

Although *Palaeorchis crassus* had low prevalence throughout the study period, fully developed infective cercariaeum stages were found in all samples. Evans (1978) examined *Bithynia tentaculata* for *Asymphylodora kubanicum*, which is a close relative of *P. crassus*. He also noted that infective larval stages were present all year round. The *Asymphylodora* life cycle also includes a cercariaeum stage which usually encysts in gastropods (Broek & Jong 1979). The cercariaeum of *P. crassus* is presumably transferred to the next host when the clam is eaten. A more fragile shell found in *P. crassus*-infected clams would favour transmission to the second intermediate host. More studies need to be carried out to determine the life cycle of *P. crassus*.

Transmission of *Bunodera luciopercae* and *Phyllodistomum elongatum* from the clam to the next host is via free-swimming, emerging cercariae which are eaten by the second intermediate host and definitive host, respectively. Large, cystophorous cercariae of *P. elongatum* resemble food items; the same strategy is known for other species of *Phyllodistomum* and for azygiids (Ivantsiv & Kurandina 1985).

Holopainen & Hanski (1986) reported the present *Pisidium amnicum* population to be semelparous and have suggested that semelparity exists when environmental conditions are optimal and maximum size is achieved prior to reproduction. However, semelparity of the present population is more likely caused by parasitic castration (Holopainen et al. 1997): clams are castrated before the second brood. According to Taskinen & Valtonen (1995), *Anodonta piscinalis* is free of trematode infections prior to maturation. They speculated that the cost of being infected is lower in adult clams and immunity may disappear during maturation. A mechanism to ensure the reproduction of the host individual may also be involved in the relationship between *P. amnicum* and its digenean parasites. A combination of ecological and/or immunological factors which prevent infection in juvenile clams together with parasitic castration after the production of the first brood of young clams might lead to semelparity of the host population, providing that the level of parasitism is high. This might be the situation in the clam population studied. No clam which was both gravid and parasitized was ever found and no parasitized clam retained its gonads.

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