

ASPECTS OF THE ECOLOGY AND NATURAL HISTORY OF *PARAERGASILUS RYLOVI*  
(COPEPODA, ERGASILIDAE) PARASITIC IN UNIONIDS OF FINLAND

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**ABSTRACT:** The distribution of *Paraergasilus rylovi* in 17 populations of unionids was investigated. In 1 unionid population, the parasite was studied regarding host age, size, sex, and the reproductive period (occurrence of egg sacs). Results from pooled material from the years 1987–1989 and 1996 (southern Finland, 11 populations) indicated that *Anodonta piscinalis* ( $n = 1,359$ ) is the main host (total mean prevalence 71% and intensity  $\pm$  SE of infection  $16.4 \pm 0.6$ ). *Pseudanodonta complanata* ( $n = 106$ ) was infected occasionally (3% and  $1.3 \pm 0.3$ ), whereas *Unio pictorum* ( $n = 108$ ) and *U. tumidus* ( $n = 17$ ) were not infected. Results from 17 *A. piscinalis* populations showed that *P. rylovi* occurs in southern Finland but not in northern Finland. In *A. piscinalis*, the mean intensity of infection was higher in lake populations than in river populations. Both host age and length had a negative relationship with the intensity of *P. rylovi* infection. Host sex did not affect the intensity of infection. Egg sacs of *P. rylovi* were found from June to August. There was a tendency for higher intensities of infection in autumn. Infection by the digenean *Rhipidocotyle fennica* had no effect on the intensity of *P. rylovi* infection.

The ergasilid copepod *Paraergasilus rylovi* Markewitsch 1937 was redescribed by Chernysheva and Purasjoki (1991) on the basis of planktonic specimens and mature specimens parasitic on the unionid *Anodonta piscinalis* Nilsson, 1823 in Lake Vriero, St. Petersburg district. Markewitsch (1937) and Markewitsch and Kusmorska (1937) described the species from planktonic material from brackish water from the northern Caspian Sea, but subsequent findings have been from freshwater, with mature specimens being found from nostrils or gills of fishes (e.g., Kostarev, 1977). However, Titar and Chernogorenko (1982) found their species from *A. piscinalis*. Because the type material used by Markewitsch (1937) has been destroyed, and because of uncertainties of original description, it is possible that instead of *P. rylovi* Markewitsch, Chernysheva and Purasjoki (1991) described *P. markewitsch* Titar and Chernogorenko 1982. Before this taxonomic problem is solved, we use the name *P. rylovi*. Aspects of the biology of *P. rylovi* are largely unknown (but see Taskinen and Saarinen, 1999; Saarinen and Taskinen, 2003a). Ergasilids are ectoparasites of many freshwater fish (Bauer et al., 1973), and *P. rylovi* is the only ergasilid known to infect freshwater mollusks.

The host of *P. rylovi*, *A. piscinalis*, matures at 2–4 yr of age and reproduces annually (Haukioja and Hakala, 1978a; Bauer, 1994), with a maximum life span of more than 15 yr (Økland, 1963; Negus, 1966; Haukioja and Hakala, 1978a). Spawning takes place in early summer, and fertilized eggs are stored in the outer gill blades of females, where they develop into glochidia larvae (Jirka and Neves, 1992). After release, glochidia attach to a fish host for a few weeks before assuming a benthic life. Unionids can constitute up to 95% of lake benthic biomass (Økland, 1963) and have a remarkable impact on nutrient cycling in lakes (Kasprzak, 1985).

The aim of this study was to investigate the host specificity and the geographic distribution of *P. rylovi* in 17 unionid populations in Finland, including populations of 4 species (*A. piscinalis*, *Pseudanodonta complanata* Rösmässler, 1835, *Unio pictorum* Linnaeus, 1758, and *U. tumidus* Philipsson, 1788). In *A. piscinalis*, the prevalence and intensity of infection in rela-

tion to host age, length, sex, and habitat were studied. In addition, seasonal differences in the intensity of infection and the reproductive period (occurrence of egg sacs) of *P. rylovi* were examined. Finally, the intensity of *P. rylovi* infection was analyzed in relation to the occurrence of the digenean parasite *Rhipidocotyle fennica* Gibson, Valtonen, and Taskinen 1992.

## MATERIALS AND METHODS

During 1987, 1988, and 1989, unionids were collected from the littoral (1–2 m deep) and sublittoral (3–4 m deep) zones of Lake Saravesi, Finland, using a bottom dredge. For a description of the collection site, see Taskinen and Valtonen (1995). In 1987, 344 *A. piscinalis*, 19 *P. complanata*, and 11 *U. pictorum* were collected. In 1988, the corresponding sample sizes were 151, 12, and 7, and in 1989 they were 85, 14, and 3. Unionids were collected at different times of the year. The 1987 data collections (sampling month followed by numbers of *A. piscinalis* collected in parentheses) were May (98), June (102), July (76), August (21), and October (45). The same data for 1988 were July (43), August (63), and September (23) and those for 1989 were March (28) and November (33). These samples represent the same samples used by Taskinen et al. (1994) to study the seasonality of *R. fennica* infections in *A. piscinalis*. However, the November and December 1987 samples, the December 1988 sample, and the January 1989 samples used by Taskinen et al. (1994) were excluded from this study because those unionids were kept for several days at a higher temperature than the lake water, which may have reduced the number of *P. rylovi* (Saarinen and Taskinen, 2003a). For similar reasons, the monthly sample sizes of *A. piscinalis* given above may differ from those presented by Taskinen et al. (1994) because those unionids exposed to laboratory conditions for more than 3 days were excluded from the study data.

Monthly collections (numbers of *A. piscinalis* collected in parentheses) were also made in Lake Saravesi in 1996 by scuba diving: May (42), June (18), and August (25). The 1996 material from lakes Saravesi, Jyväsjärvi, and Tuomiojärvi (Table I) was used in part by Saarinen and Taskinen (2003b) to study the burrowing behavior of 3 unionid species. The material from 1996 from lakes Alvajärvi, Jyväsjärvi, and Saravesi was used in part by Taskinen and Saarinen (1999) to study the relationship between the maturity of *A. piscinalis* and the abundance

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TABLE I. *Anodonta piscinalis* collected between May and October 1996 from 17 sites (population, location) in southern and northern Finland; prevalence of infection and mean intensity of *Paraergasilus rylovi* infection.

	Population code	Population	No. collected	% Prevalence	Mean intensity $\pm$ SE
Southern Finland	1	River Siikakoski, Konnevesi	37	21.6	1.2 $\pm$ 0.2
	2	River Pesiäissalmi, Laukaa	54	20.4	2.2 $\pm$ 0.6
	3	Lake Saravesi, Laukaa	85	98.8	25.8 $\pm$ 2.1
	4	River Kuusaankoski, Laukaa	138	21.7	1.9 $\pm$ 0.3
	5	Lake Ahveninen, Laukaa	57	0	
	6	Lake Vuojärvi, Laukaa	7	0	
	7	Lake Jyväsjärvi, Jyväskylä	161	91.3	14.9 $\pm$ 1.2
	8	Lake Alvajärvi, Jyväskylä	154	97.4	12.9 $\pm$ 0.8
	9	Lake Palokkajärvi, Jyväskylä	12	83.3	38.1 $\pm$ 5.1
	10	Lake Tuomiojärvi, Jyväskylä	55	47.3	3.5 $\pm$ 0.8
	11	Lake Tuomaanlampi, Vaajakoski	42	83.3	4.9 $\pm$ 0.6
Northern Finland	12	Lake Kuivasjärvi, Oulu	20	0	
	13	Lake Hyrynjärvi, Hyrynsalmi	20	0	
	14	Lake Ranuanjärvi, Ranua	20	0	
	15	Lake Siikalampi, Taivalkoski	13	0	
	16	Lake Oivankijärvi, Kuusamo	7	0	
	17	River Kemijoki, Rovaniemi	20	0	

of *P. rylovi*. Seasonality in the intensity of *P. rylovi* infection was studied using the above-noted samples from Lake Saravesi collected during 1987–1989 and 1996.

The presence of *P. rylovi* in hosts was determined by pressing the host gill tissues between 2 large glass plates and observing them under a dissection microscope with transmitted light. For each *P. rylovi*, the occurrence of egg sacs was used to determine reproductive state. Unionid gonads were examined under a dissection microscope for the presence of larval digeneans and to determine the sex of the host. Between May and October 1996, 902 *A. piscinalis* were collected from 17 locations in Finland by scuba diving (Table I) to study the host specificity and geographic distribution of the parasite. Populations coded 1–11 (see Table I) flow via Lake Päijänne to the Gulf of Finland, Baltic Sea. Populations coded 12–15 and 17 flow into the Gulf of Bothnia, Baltic Sea, and population no. 16 flows into the White Sea, Arctic Ocean. The occurrence of *P. rylovi* was determined as described above. Eleven of the study locations were in southern Finland, within 100 km of the city of Jyväskylä. The southern populations contained *A. piscinalis* ( $n = 802$ ), *P. complanata* ( $n = 87$ ), *U. pictorum* ( $n = 64$ ), and *U. tumidus* ( $n = 17$ ). Six of the locations were in northern Finland, between the cities of Oulu and Rovaniemi. The northern populations contained only *A. piscinalis* ( $n = 100$ ).

The host specificity of *P. rylovi* was studied by examining all the collections noted above. However, the 1996 collections from northern Finland were excluded because the parasite did not occur in that geographic area (see below). Seven populations, 4 of which were lakes (population codes 3, 7, 8, and 11 in Table I) and 3 rivers (population codes 1, 2, and 4 in Table I), were sampled in May 1996 (a total of 399 *A. piscinalis*) to study the effect of habitat (stagnant vs. flowing water) on the intensity of *P. rylovi* infection. Data were analyzed using 1-way analysis of variance (ANOVA), using population as a factor and habitat (stagnant or flowing) as a contrast.

In September ( $n = 73$ ) and October ( $n = 22$ ) 2002, *A. pis-*

*cinalis* were collected from Lake Saravesi by scuba diving. The unionids were examined for parasites, aged (see Haukioja and Hakala, 1978b), and their length measured in the laboratory. These data were used to study the relationship between the intensity of *P. rylovi* infection and age, size, and sex of the host. The same data were used by Saarinen and Taskinen (2003a) as a field reference sample in an experimental study of the effect of water temperature on the occurrence of *P. rylovi*. The effect of host age on the intensity of *P. rylovi* was analyzed using 1-way analysis of covariance (ANCOVA), using month as a factor and age as a covariate. The effect of host length on the intensity of *P. rylovi* was analyzed similarly. The effect of sex of the host on the intensity of *P. rylovi* was analyzed using 1-way ANCOVA, using sex as a factor and length as a covariate. *Anodonta piscinalis* specimens heavily infected by the digenean *R. fennica* (see Taskinen et al., 1994) were excluded from the analysis regarding sex dependence because this digenean castrates its hosts (Taskinen and Valtonen, 1995). Only the sample collected in September contained an adequate number of both female and male unionids for this analysis.

Logistic regression was used to analyze the relationship between the occurrence of egg sacs in *P. rylovi* and month, unionid length, and the interaction term “mo  $\times$  unionid length” in hosts collected from Lake Saravesi in June and August 1996. Month was included as an independent categorical covariate in the model and length as a continuous covariate. An automated forward stepwise variable selection procedure was used to select the model that best fit the data. By comparing hierarchical sets of regression models, the significance of interaction and main effects was calculated using likelihood ratio statistics (Forward LR). The variable selection was then repeated using automated backward stepwise elimination procedure (Backward LR). If the 2 procedures did not result in the same model, then the terms that differed were tested for their significance using improvement  $\chi^2$ -test. If the term was significant, it was included in the model. Differences between years in the mean intensity of *P. rylovi* infection were analyzed using the 1987, 1988, and

TABLE II. Number of studied individuals, prevalence, and mean intensity of infection of *Paraergasilus rylovi* in 4 species of unionids studied during 1987–1989 and 1996 from 11 populations from southern Finland.

Species	No. studied	% Prevalence	Mean intensity $\pm$ SE
<i>Anodonta piscinalis</i>	1,359	71.2	16.4 $\pm$ 0.6
<i>Pseudanodonta complanata</i>	106	2.8	1.3 $\pm$ 0.3
<i>Unio pictorum</i>	108	0.0	0.0
<i>Unio tumidus</i>	17	0.0	0.0

August 1996 samples from Lake Saravesi with 1-way ANOVA using month as a factor. The seasonality (=monthly differences) in the mean intensity of *P. rylovi* infection was analyzed using data from Lake Saravesi, with 1-way ANOVA, using month as a factor. Samples from 1987–1989 and 1996 were analyzed separately for monthly differences in the intensity of *P. rylovi* infection. The effect of infection with *R. fennica* on the intensity of *P. rylovi* infection was studied by combining all *A. piscinalis* collections from 1987–1989, 1996, and 2002 in Lake Saravesi. The relationship was analyzed using 2-way ANCOVA, using year and *R. fennica* infection as factors and length as a covariate. Means are given with  $\pm 1$  SE. Statistical analyses were performed using SPSS statistical package (SPSS Inc. Chicago, Illinois).

## RESULTS

Of the 4 unionids studied, the main host for *P. rylovi* was *A. piscinalis*. Among the 11 southern Finland populations in 1996, the mean prevalence and intensity of infection varied from 0 to 97.4% and from 0 to 38.1  $\pm$  0.3, respectively. In the material pooled over populations (southern Finland, 11 populations) and year (1987–1989, 1996) the mean prevalence and intensity of infection in *A. piscinalis* was 71.2% and 16.4  $\pm$  0.6, respectively (Table II). The parasite occasionally infected *P. complanata*. However, the mean prevalence and intensity ( $\pm$ SE) of infection in the pooled material were only 2.8% and 1.3  $\pm$  0.3, respectively. *Unio pictorum* and *U. tumidus* were not infected by *P. rylovi* (Table II). In data collected in 1996 from 17 *A. piscinalis* populations, *P. rylovi* occurred in southern Finland but not in northern Finland (Table I). Between-year differences in the intensity of *P. rylovi* infection were studied using samples collected in August 1987, 1988, and 1996 from Lake Saravesi. The mean intensity of *P. rylovi* differed between years (1-way ANOVA,  $F_{2,51} = 4.521$ ,  $P = 0.016$ ) being 12.5  $\pm$  3.0, 19.8  $\pm$  4.5, and 24.6  $\pm$  2.7, respectively. No clear seasonality in the mean intensity of *P. rylovi* infection was evident despite a tendency for increasing intensities toward autumn (Fig. 1). In 1987, monthly intensities varied significantly (1-way ANOVA,  $F_{3,110} = 6.619$ ,  $P < 0.001$ ). The intensity decreased from May to July but increased from July to October. In 1988, the intensity of infection increased from July to September (1-way ANOVA,  $F_{2,32} = 7.113$ ,  $P = 0.003$ ). In 1989, *P. rylovi* intensity in November was twice that in March (1-way ANOVA,  $F_{1,42} = 8.182$ ,  $P = 0.007$ ). In 1996, May, June, and August did not differ from each other in the intensity of infection (1-way ANOVA,  $F_{2,81} = 1.693$ ,  $P > 0.1$ ).

The effect of habitat (stagnant water, lake habitat vs. flowing

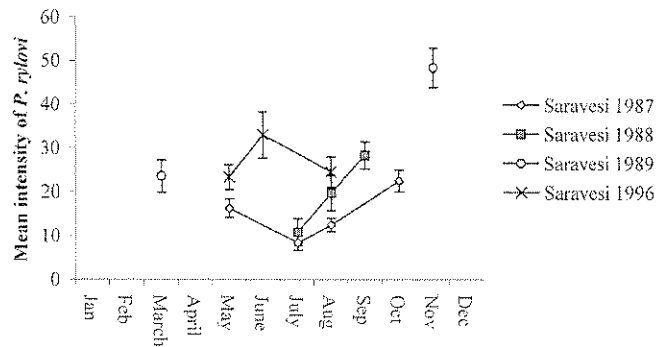


FIGURE 1. Monthly mean intensity ( $\pm$ SE) of *Paraergasilus rylovi* infection in *Anodonta piscinalis* in Lake Saravesi during 1987–1989 and 1996.

water, river habitat) on the intensity of *P. rylovi* was statistically significant (1-way ANOVA, contrast test,  $t = 12.344$ ,  $P < 0.001$ ). The mean intensity of *P. rylovi* was lower in rivers (1.9  $\pm$  0.3) as compared with lakes (14.7  $\pm$  1.0) (Fig. 2). The intensity of *P. rylovi* infection with respect to host age and size was studied using the material collected from Lake Saravesi in September and October 2002. Unionid age had an effect on the intensity of *P. rylovi* infection (1-way ANCOVA,  $F_{1,92} = 4.513$ ,  $P = 0.036$ ) as did host length (1-way ANCOVA,  $F_{1,92} = 10.100$ ,  $P = 0.002$ ). Both had a negative relationship to the intensity of *P. rylovi* infection (covariate age,  $B = -1.635$ ,  $t = -2.124$ ,  $P = 0.036$ ; covariate length,  $B = -0.660$ ,  $t = -3.178$ ,  $P = 0.002$ ) (Fig. 3a, b). Female and male unionids collected in September 2002 did not significantly differ in *P. rylovi* infection intensity (1-way ANCOVA,  $F_{1,47} = 0.109$ ,  $P = 0.743$ ).

*Rhipidocotyle fennica* infection did not have an effect on the mean intensity of *P. rylovi* infection in Lake Saravesi in 1987–1989, 1996, and 2002 (2-way ANCOVA,  $F_{1,338} = 0.001$ ,  $P = 0.980$ ). Infection intensities of *P. rylovi* differed between years (2-way ANCOVA,  $F_{4,338} = 21.362$ ,  $P < 0.001$ ). The interaction term “yr  $\times$  *Rhipidocotyle fennica* infection” was not significant

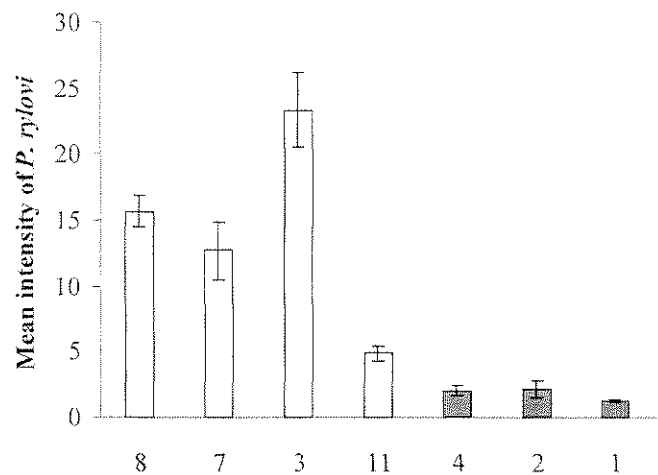


FIGURE 2. The mean intensity ( $\pm$ SE) of *Paraergasilus rylovi* infection in *Anodonta piscinalis* in 4 lakes (open bars) and 3 rivers (hatched bars) in May 1996. Numbers below bars refer to the populations listed in Table I.

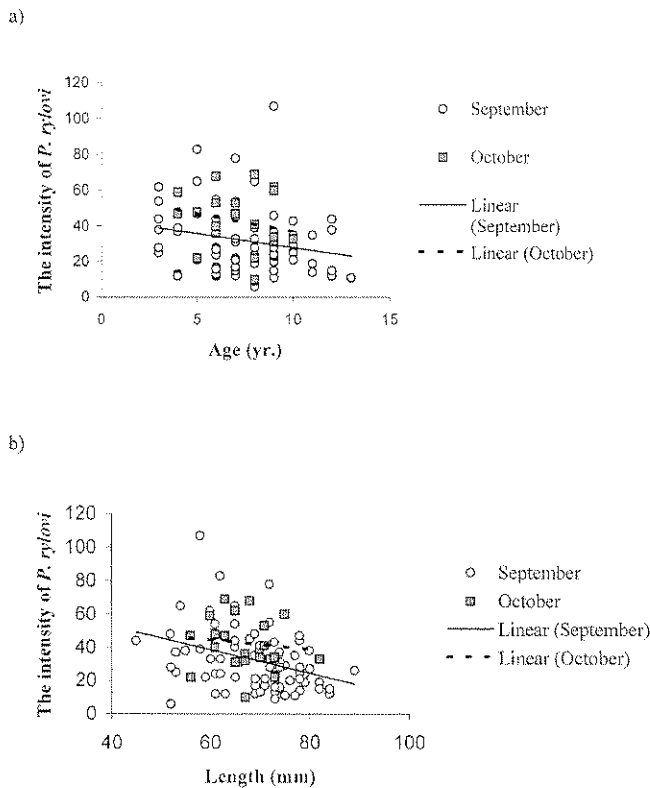


FIGURE 3. The relationship between the intensity of *Paraergasilus rylovi* infection in Lake Saravesi in September and October 2002 and (a) the age and (b) the length of *Anodonta piscinalis*. Lines represent results of linear regressions.

( $F_{4,338} = 0.798$ ,  $P = 0.527$ ). Host length had a negative relationship with the intensity of *P. rylovi* (length,  $B = -0.231$ ,  $t = -2.474$ ,  $P = 0.013$ ).

*Paraergasilus rylovi* females in Lake Saravesi during 1987–1989 and 1996 carried egg sacs during June, July, and August, with the highest prevalences of egg sacs being found in June and July (Fig. 4). There were large differences between years in the occurrence of egg sacs. For example, egg sacs seemed to be more frequent in 1996 than in 1987 or 1988. When analyzing the effect of month (June, August) and host size in Lake Saravesi for 1996 on the occurrence of *P. rylovi* egg sacs, the logistic regression model included only the constant, indicating that the occurrence of egg sacs was not affected by month or host length. Egg sacs were not found in *P. rylovi* collected from *P. complanata* (n studied between June and August = 54).

## DISCUSSION

*Paraergasilus rylovi* was abundant in *A. piscinalis*, whereas the other unionid bivalves were either only occasionally infected (*P. complanata*) or not infected (*U. pictorum*, *U. tumidus*). Those *P. complanata* harboring the parasite were found within a dense *A. piscinalis* population. In addition, no *P. rylovi* was found with egg sacs in *P. complanata*, suggesting that the parasite may not be able to reproduce in *P. complanata*. These results suggest that *P. rylovi* is specialized to infect *A. piscinalis*

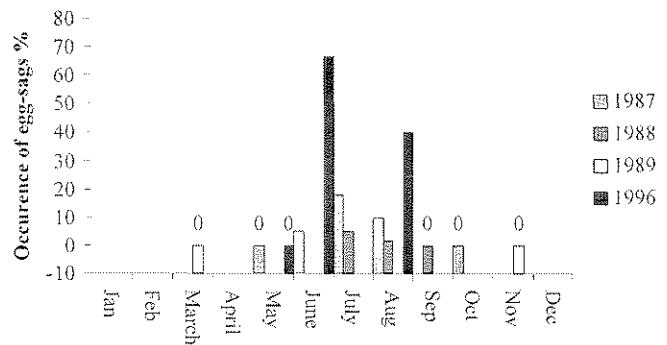


FIGURE 4. The occurrence of *Paraergasilus rylovi* with egg sacs in *Anodonta piscinalis* from Lake Saravesi during 1987–1989 and 1996.

only. This, in turn, means that reciprocal evolution, i.e., coevolution, could be predicted between *P. rylovi* and *A. piscinalis*.

Host specificity of 3 other ergasilids, parasites of the fishes *Perca fluviatilis*, *Rutilus rutilus*, and *Coregonus* sp., were examined in the study area by Tuuha et al. (1992). In an extensive investigation including 4 fish populations and a total of 2,230 fishes, *Ergasilus sieboldi* was restricted entirely to *P. fluviatilis* and *E. briani* and *Neoergasilus japonicus* to *R. rutilus*. *Paraergasilus longidigitus* infected both *P. fluviatilis* and *R. rutilus*, but none of the ergasilids infected *Coregonus* sp. (Tuuha et al., 1992). However, Pojmanska (1984) did observe *E. sieboldi* to infect several species in Poland. Thus, the degree of host specificity may vary among various geographic areas, and specificity of *P. rylovi* may also vary geographically.

Although a frequent and abundant parasite in southern Finland *A. piscinalis* populations, the parasite was absent from northern Finland. Thus, both the unionid species and the geographic region affect the occurrence and abundance of *P. rylovi*. The only other location from which *P. rylovi* has been reported in unionids so far is the Leningrad district (St. Petersburg) in Russia (Chernysheva and Purasjoki, 1991). If the distribution of *P. rylovi* is limited by chance of introduction to new areas, it is not surprising that southern Finland populations harbor the parasite, rather than the northern populations, because hydrologically they and the St. Petersburg drainage basin both empty into the Gulf of Finland, Baltic Sea. The drainage areas of the northern populations flow in several directions, i.e., to the Gulf of Bothnia, Baltic Sea, or to White Sea, Arctic Ocean. However, we cannot exclude the possibility that, for example, the shorter summers and cooler waters in the north prevent successful reproduction of *P. rylovi* thus restricting the parasite to southern areas.

The present results indicate that the stagnant waters of the littoral zones of lakes are optimal habitats for *P. rylovi*, whereas the flowing waters of rivers provide a suboptimal environment. This is probably not due to higher host density in the littoral zones of lakes because the unionid density is usually much higher in rivers. For example, in the current study area, it took 60 min to collect 50 unionids from Lake Saravesi, whereas only 15 min to do so in River Kuusaankoski (data not shown). Gee and Davey (1986) reported lower levels of infection by the copepod *Mytilicola intestinalis* in blue mussels, *Mytilus edulis*, in turbulent regions as compared with calm regions. They hypothesized that this resulted from the essentially passive nature

of the infection process and that the poor-swimming, short-lived infective stages of *M. intestinalis* enter the mussel via filtration. A similar process might explain the lower prevalence and intensity of *P. rylovi* parasitism in rivers compared with lakes in this study. In addition, increased stream velocity has also been found to decrease the abundance and prevalence of fish ergasilid copepod, *E. celestis*, in wild eels, *Anguilla rostrata* (Barker and Cone, 2000). Perhaps in rivers, *P. rylovi* larvae are flushed away before they become infective.

The egg sacs of *P. rylovi* in Lake Saravesi occurred during the warm-water period from June to August. The reproductive period of *E. briani* occurs at the same period in Lake Saravesi (Tuuha et al., 1992). The monthly size distributions of *E. briani* suggested 2 generations per year, so that the overwintering parasite population produces eggs in June, and copepods derived from these eggs attack fish in July, producing a second generation that infects fish from August onward, then overwinter in fish, and produce eggs the next June (Tuuha et al., 1992).

In this study, there was a tendency, seasonally, for higher intensities of infection to occur in late autumn in Lake Saravesi. This is in line with the occurrence of egg production between June and August. Eggs hatched in summer produce larvae that will become infective adults during the autumn, which could result in an increase in the intensity of infection at that time.

*Paraergasilus rylovi* probably enter the host via filtration, in a fashion similar to that of *M. intestinalis* in *M. edulis*. Larger sized *M. edulis* with larger fields of filtration (Davey and Gee, 1976) harbor more *M. intestinalis* (Gee and Davey, 1986). A similar size (and age)-dependent pattern of infection is found in the prevalence of digenean *R. fennica* in *A. piscinalis* (Taskinen and Valtonen, 1995). Therefore, it was surprising that there was a negative relationship between size (and age) of the host and intensity of *P. rylovi* infection. The behavior of the host might change with age and size so that the exposure to parasitism decreases. For example, Saarinen and Taskinen (2003b) observed the burrowing depth of *A. piscinalis* to change with size so that larger individuals were more visible than smaller individuals. Alternatively, the increasing prevalence of *R. fennica* with size (age) of *A. piscinalis* (Taskinen and Valtonen, 1995) might have a negative effect on *P. rylovi*. The present results yielded no association between *P. rylovi* and *R. fennica*, suggesting that the last hypothesis may not be correct. However, experimental studies are needed to resolve alternative explanations.

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#### LITERATURE CITED

- BARKER, D. E., AND D. K. CONE. 2000. Occurrence of *Ergasilus celestis* (Copepoda) and *Pseudodactylogyrus anguillae* (Monogenea) among wild eels (*Anguilla rostrata*) in relation to stream flow, pH and temperature and recommendations for controlling their transmission among eels. *Aquaculture* 3-4: 261-274.
- BAUER, G. 1994. The adaptive value of offspring size among freshwater mussels (Bivalvia, Unionidae). *Journal of Animal Ecology* 63: 933-944.
- BAUER, O. N., V. A. MUSSELIUS, AND Y. A. STRELKOV. 1973. Diseases of pond fishes. Israel Program for Scientific Translations, Jerusalem, Israel, 312 p.
- CHERNYSHEVA, N. B., AND K. J. PURASJOKI. 1991. A redescription of *Paraergasilus rylovi* Markevich, 1937 (Copepoda, Ergasilidae). *Systematic Parasitology* 20: 165-172.
- DAVEY, J. T., AND J. M. GEE. 1976. The occurrence of *Mytilicola intestinalis* Steuer, an intestinal copepod parasite of *Mytilus*, in the south-west of England. *Journal of the Marine Biological Association of the United Kingdom* 56: 85-94.
- GEE, J. M., AND J. T. DAVEY. 1986. Experimental studies on the infestation of *Mytilus edulis* (L.) by *Mytilicola intestinalis* Steuer (Copepoda, Cyclopoida). *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 42: 265-271.
- HAUKIOJA, E., AND T. HAKALA. 1978a. Life-history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia* 35: 253-266.
- , AND ———. 1978b. Measuring growth from shell rings in populations of *Anodonta piscinalis* (Pelecypoda, Unionidae). *Annales Zoologici Fennici* 15: 60-65.
- JIRKA, K. J., AND R. J. NEVES. 1992. Reproductive biology of four species of freshwater mussels (Mollusca: Unionidae) in the New River, Virginia and West Virginia. *Journal of Freshwater Ecology* 7: 35-44.
- KASPRZAK, K. 1985. Occurrence and role of the family Unionidae (Mollusca, Bivalvia) in the eutrophic Lake Zbechy and its outflow canal. *Acta Hydrobiologica* 27: 351-370.
- KOSTAREV, G. F. 1977. Bream and pike-perch infected by *Paraergasilus rylovi*, Markewitsch 1937. *Biologiya Vnutrennikh Vod. Informatsionnyj B'ulleten* 36: 76-77. [In Russian.]
- MARKEWITSCH, A. P. 1937. Copepoda parasitica of freshwaters of USSR. *Izdatelstvo Akademii Nauk Ukrainskoj SRR, Kiev, Ukraine*, 259 p. [In Russian.]
- , AND A. P. KUSMORSKA. 1937. *Paraergasilus rylovi* Markewitsch, a new representative of parasitic copepods from the Caspian Sea. *Naukovi Zapiski, Biologichnij Zhurnal* 3: 381-397. [In Ukrainian, English Summary.]
- NEGUS, C. L. 1966. A quantitative study of growth and production of unionid mussels in the river Thames at Reading. *Journal of Animal Ecology* 35: 513-532.
- ØKLAND, J. 1963. Notes of population density, age distribution, growth, and habitat of *Anodonta piscinalis* Nils. (Moll. Lamellibr.) in a eutrophic Norwegian lake. *Nytt Makasin for Zoologi* 11: 19-43.
- POJMANSKA, T. 1984. An analysis of seasonality of incidence and maturation of some fish parasites, with regard to thermal factor. 1. General methods. *Ergasilus sieboldi* Nordmann, 1932. *Acta Parasitologica Polonica* 29: 217-228.
- SAARINEN, M., AND J. TASKINEN. 2003a. Reduction in the level of infection of the bivalve *Anodonta piscinalis* by the copepod *Paraergasilus rylovi* using high temperature and low oxygen. *Journal of Parasitology* 89: 1167-1171.
- , AND ———. 2003b. Burrowing and crawling behaviour of three species of unionidae in Finland. *Journal of Molluscan Studies* 69: 81-86.
- TASKINEN, J., AND M. SAARINEN. 1999. Increased parasite abundance associated with reproductive maturity of the clam *Anodonta piscinalis*. *Journal of Parasitology* 85: 588-591.
- , AND E. T. VALTONEN. 1995. Age-, size-, and sex-specific infection of *Anodonta piscinalis* (Bivalvia: Unionidae) with *Rhipidocotyle fennica* (Digenea: Bucephalidae) and its influence on host reproduction. *Canadian Journal of Zoology* 73: 887-897.
- , ———, AND T. MÄKELÄ. 1994. Quantity of sporocysts and seasonality of two *Rhipidocotyle* species (Digenea: Bucephalidae) in *Anodonta piscinalis* (Mollusca: Bivalvia). *International Journal for Parasitology* 24: 877-886.
- TITAR, V. M., AND M. I. CHERNOGORENKO. 1982. A new species of *Paraergasilus* Markewitsch, 1937 (Copepoda: Ergasilidae) from a freshwater bivalve mollusk *Anodonta piscinalis* Nils. (Mollusca: Unionidae). *Parazity i parasitozy cheloveka i zivotnykh. Sbornik Nauchnykh Trudov. Naukova Dumka, Kiev, Ukraine*, p. 214-218. [In Russian, English Summary.]
- TUUHA, H., E. T. VALTONEN, AND J. TASKINEN. 1992. Ergasilid copepods as parasites of perch *Perca fluviatilis* and roach *Rutilus rutilus* in Central Finland: Seasonality, maturity and environmental influence. *Journal of Zoology* 228: 405-422.