THE LIFE CYCLE AND SEASONAL CHANGES IN THE OCCURRENCE OF *POMPHORHYNCHUS LAEVIS* (PALAEACANTHOCEPHALA, POMPHORHYNCHIDAE) IN A SMALL ISOLATED LAKE

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Summary:

In a small isolated lake in Slovakia, the fish acanthocephalan *Pomphorhynchus laevis* using *Gammarus balcanicus* and the minnow *Phoxinus phoxinus*, respectively, as its intermediate and final hosts, represented a dominant helminth species. Its prevalence and intensity of infection in fish showed no significant variation during a year fluctuating above the mean values of 89 % and 6.6 worms per fish. The mean prevalence of *P. laevis* larvae in *Gammarus* was 41.4 % with a maximum in the late summer and autumn; individual crustaceans were infected by 1-9 larvae. There was one generation of *P. laevis* per year. Following up an annual cycle, an occurrence of new infections of *Gammarus* culminated in October and in the next May for *Phoxinus*. The sex ratios of both the adults and larvae of acanthocephalans were near unity but favoured slightly males in spring and autumn. The distribution of *P. laevis* in minnows and crustaceans was highly aggregated and fitted with the negative binomial model. The spatial distribution analysis of parasites along the fish alimentary tract showed a clear preference of *P. laevis* for its proximal half, with the maximum numbers in the site of the first intestinal loop. Immature worms of both sexes predominated in the proximal region and moved slightly down the alimentary tract during their growth and maturation.

KEY WORDS : *Pomphorhynchus laevis*, *Phoxinus phoxinus*, *Gammarus balcanicus*, life cycle, seasonal occurrence, spatial distribution.

Résumé : CYCLE DE VIE ET CHANGEMENTS SAISONNIERS DE L'ÉMERGENCE DE *POMPHORHYNCHUS LAEVIS*

(PALAEACANTHOCEPHALA, POMPHORHYNCHIDAE) DANS UN PETIT LAC ISOLÉ

Dans un petit lac isolé en Slovaquie, une espèce dominante parmi les helminthes est l'acanthocéphale de poisson *Pomphorhynchus laevis* dont l'hôte intermédiaire est *Gammarus balcanicus* et l'hôte définitif *Phoxinus phoxinus*. Dans les poissons, ni la prévalence ni l'intensité d'infection ne varient significativement pendant l'année autour de leur valeur moyenne : 89 % des poissons sont infectés avec une moyenne de 6,6 parasites par poisson. Chez *Gammarus*, la prévalence moyenne est de 41,4 % avec un maximum annuel à la fin de l'été et en automne. Une à neuf larves peuvent infecter un crustacé. Il y a seulement une génération de *P. laevis* par an. Suivant un cycle annuel, l'émergence de la nouvelle infection du *Gammarus* culmine en octobre et celle de *Phoxinus* en mai. Le sex-ratio chez les adultes comme chez les larves est proche de un; cependant, les mâles sont légèrement plus nombreux au printemps et en automne. La répartition de *P. laevis* dans le vairon et dans les crustacés est très agrégée en suivant le modèle binomial négatif. L'analyse de la distribution spatiale des parasites le long du tractus digestif montre clairement une préférence pour la moitié proximale avec un maximum de densité dans la première boucle intestinale. Les vers immatures prédominent dans la région proximale et progressent lentement le long du tube digestif au cours de leur croissance et de leur développement sexuel.

MOTS CLÉS : *Pomphorhynchus laevis*, *Phoxinus phoxinus*, *Gammarus balcanicus*, cycle de vie, émergence saisonnière, distribution spatiale.

INTRODUCTION

Pomphorhynchus laevis (Zoega in Müller, 1776) is a widespread acanthocephalan parasite of many freshwater and/or brackish European fishes (e.g. Yamaguti, 1963 ; Kakacheva-Avramova, 1977; Kennedy *et al.*, 1989; Moravec & Scholz, 1991). In the freshwaters of Europe, preferred final hosts of this parasite are chub *Leuciscus cephalus* (L., 1758) and barbel *Barbus barbus* (L., 1758). However, *P. laevis* is able to complete its live cycle also in other fish hosts like the minnow *Phoxinus phoxinus* (L., 1758) when

occurring in an isolated lake (Dudiňák & Šnábel, 2001). The present study analyses seasonal changes of the *P. laevis* occurrence within both the fish and crustacean hosts (*P. phoxinus* and *Gammarus balcanicus* Schäferna, 1922, respectively) in the mentioned lake in Slovakia. Seasonal changes in the sex ratio and a maturation process of *P. laevis* and its spatial distribution within the fish alimentary canal were spotted as well.

MATERIAL AND METHODS

Eight samples of crustaceans and seven samples of fish were taken from February to November 2001 in the Small Vihorlat Lake, Eastern Slovakia (Table I). The Small Vihorlat Lake (named also Malé Morské oko) is the natural forest lake of mesotrophic

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character with the water surface of about 4,000 m² and the maximum depth of 3.5–4 m. The lake is situated in the centre of Vihorlat Mountains area (22° 12' E, 48° 55' N), 727 m above the sea level (Terek & Švajdová, 1999). It is filled by a single spring-water flow and has no surface water outlet. The lake is covered by ice from the end of November to March; in summer a water overheating and a considerable decrease of the water surface may occur. The lake is inhabited only by two fish species: minnow, which predominates, and the extremely rare dwarfish form of Crucian carp *Carassius carassius* (L.). The locality is protected under the National Conservation network and the research was performed with the permission of the Ministry of Environment of the Slovak Republic.

As many as 129 minnows were fished using scoop-net (Table I) and transferred alive to the laboratory. Before the dissection, fish length and weight were determined, ranging from 62 to 120 mm (83.6 ± 8.1) and from 1.9 to 11.2 g (6.0 ± 1.9). Dissected alimentary tracts up to 74 mm long were squashed between two slides, fixed in 70 % ethanol and then cleared in lactic acid. The position of individual parasites was recorded as the percentage of the distance from the oesophagus and intestinal swelling (0 %) to the anus (100 %), reflecting also the positions of the first (34 %) and second (66 %) intestinal loops.

Parasites were divided according to the sex and maturity. The males and females were categorised into three groups, corresponding with three developmental stages: 1) Immature worms with body length up to 6 mm (female with a single ovary, males with small undeveloped testes); 2) Developing worms with body length from 6 to 12 mm with developed gonads (female with ovarian balls and/or unshelled acanthors in a body cavity, male with developed testes but undeveloped cement glands); and 3) Mature worms with body length exceeding 12 mm (female with shelled acanthors, male with well developed testes and cement glands).

A total of 614 *G. balcanicus* were sampled in the same locality using a deep net (Table I). Crustaceans were transferred alive to the laboratory and examined for *P. laevis* infection. Isolated larvae were fixed in 70 % alcohol, stained in Semichon's carmine and mounted in Canada balsam as permanent slides. Two larval stages (acanthella and cystacanth) and their sex were determined following Schmidt (1985) and Dezfuli *et al.* (1991).

Statistical comparisons were performed using non-parametrical tests (Chi-square test, Mann-Whitney test, Kruskal-Wallis ANOVA, Duncan's *post hoc* test, Spearman rank order correlation) using STATISTICA 6 (StatSoft, Inc., 2001). The degree of aggregation of adult worms per individual fish and larvae per shrimp, respectively, was qualified using the negative binomial parameter of the parasite distribution $k = (m^2 - s^2/n)/(s^2 - m)$, where s^2 = variance of the distribution, m = mean of the distribution, and n = number of hosts sampled (Elliot, 1977).

RESULTS

Data on the prevalence and intensity of infection of *P. laevis* in the final (*P. phoxinus*) and intermediate (*G. balcanicus*) hosts are summarised in Table I. The values of the *P. laevis* prevalence in minnows ranged from 77.8 to 100 % and those of the mean intensity from 4.2 to 8.2 individuals per fish. Seasonal changes of both parameters were not statistically significant (Kruskal-Wallis ANOVA of Arcsin transformed data of prevalence $H = 6.8$; $df = 6$; $P = 0.34$; Kruskal-Wallis ANOVA for intensity $H = 10.6$; $df = 6$; $P = 0.1$).

The prevalence of larval *P. laevis* in *Gammarus* varied from 30.3 to 71.4 % (Table I) and its seasonal changes were significant (Kruskal-Wallis ANOVA of Arcsin transformed data of prevalence $H = 47.3$; $df = 7$; $P < 0.001$).

Host Date (2001)	<i>Phoxinus phoxinus</i>			<i>Gammarus balcanicus</i>		
	Collected/ infected hosts	P (%)	II (min-max)	Collected/ infected hosts	P (%)	II (min-max)
13 February	3/3	100.0	8.0 (2-14)	16/5	31.3	1.8 (1-3)
10 April	10/10	100.0	8.2 (2-29)	87/37	30.3	1.7 (1-5)
10 May	32/30	93.8	5.6 (1-21)	77/30	39.0	1.8 (1-5)
21 June	25/21	84.0	8.1 (1-18)	170/63	37.1	1.8 (1-6)
27 July	16/13	92.8	4.2 (1-20)	80/52	65.0	1.9 (1-7)
20 August	16/14	93.3	6.4 (1-18)	33/22	66.7	1.7 (1-6)
4 October	27/21	77.8	6.9 (1-29)	42/30	71.4	2.0 (1-9)
6 November	—/—	—	—	107/41	38.3	1.6 (1-5)
Total	129/112	88.9	6.6 (1-29)	614/254	41.4	1.8 (1-9)

Table I. – Seasonal changes in the prevalence (P) and intensity of infection (II) of *Pomphorhynchus laevis* in the fish and crustacean hosts in the Small Vihorlat Lake.

Duncan's *post hoc* analysis showed the significantly higher prevalence in July, August and October ($P < 0.01$) compared with February, April, May, June and November. A mean intensity of infection was low varying from 1.6 to 2.0 with maximum intensity nine larvae per shrimp (Table I). Seasonal changes of this parameter were not significant (Kruskal-Wallis ANOVA $H = 2.6$; $df = 7$; $P = 0.92$).

An analysis of the frequency distribution of both adult and larval acanthocephalans in individual hosts showed a negative binomial distribution (Figs 1, 2). The degree of parasite aggregation was $k = 1.15$ for fish and 0.91 for shrimps.

Comparing the proportion of the *P. laevis* males to the females found in fish (244/224) and in crustaceans (130/121), the sex ratios did not differ significantly from the value 1:1 in both the hosts (Chi-square test $\chi^2 = 0.35$; $df = 1$; $P = 0.56$ and $\chi^2 = 0.10$; $df = 1$; $P = 0.75$, respectively). Similarly, seasonal changes in the relative occurrence of *P. laevis* males and females in minnows and *Gammarus* were not significant (Chi-square test $\chi^2 = 5.63$; $df = 6$; $P = 0.4$ and $\chi^2 = 13.4$; $df = 8$; $P = 0.1$, respectively). However, seasonal trends, ascertained in the final and intermediate hosts, concurred

Fig. 1. – Frequency distribution of *P. laevis* in the final fish hosts.

Fig. 2. – Frequency distribution of *P. laevis* larvae in intermediate crustacean hosts.

Fig. 3. – Seasonal proportions of different developmental stages of *P. laevis* in fish hosts.

Fig. 4. – Seasonal proportions of acanthellae and cystacanths of *P. laevis* in crustacean hosts.

(Spearman rank order correlation $r = 0.83$; $df = 4$; $P = 0.042$). The highest relative numbers of adult and larval males were found in the spring (52.1 and 56.4 %) and the autumn (59.5 and 66.7 %) while their number fell down in the winter (37.5 and 40 %) and the summer (48.8 and 48.7 %, respectively).

A comparison of three *P. laevis* age stages sharing the alimentary canal of minnow during the year is shown in Figure 3. The frequency of immature worms increased from February to May, the maximum number of mature worms occurred in July. Developing parasites were the most frequent in June, following the maximum occurrence of immature worms in May and foregoing this of mature individuals in July. Another enhancement of developing worms appeared in the late autumn.

An examination of the frequency of the youngest and developed larvae (i.e. acanthellae and cystacanths) showed the predominance of the acanthellae in May (42.8 %) and October (42.3 %) (Fig. 4) while cystacanths predominated remarkably in the winter (100 %) and summer (93.1 %).

The distribution of acanthocephalans alongside the minnow alimentary tract regardless the worm sex and/or developmental stage is shown in Figure 5. A majority of the parasites occurred in the first third of

Fig. 5. – Distribution of *P. laevis* in the fish alimentary tract. Vertical lines indicate a location of the first and second intestinal loops.

Fig. 6. – Distribution of different developmental stages of *P. laevis* females in the fish alimentary tract. Vertical lines indicate a location of the first and second intestinal loops.

Fig. 7. – The distribution of different developmental stages of *P. laevis* males in the fish alimentary tract. Vertical lines indicate a location of the first and second intestinal loops.

the tract and the rest of them were distributed in its middle part between two intestinal loops. The occurrence of parasites in the distal third was exceptional. No significant differences between positions of males and females were found (Mann-Whitney U test; $P = 0.61$).

Considering immature worms, slightly fixed to the wall of the host intestine, and developing and mature females or males, fixed irreversibly, the microhabitats differed significantly (Kruskal-Wallis ANOVA; $H = 51.1$; $df = 2$; $P < 0.001$). Duncan's *post hoc* analysis showed that immature acanthocephalans occupied the proximal part of the alimentary tract and this preference was more pronounced in females than males (Figs 6, 7). Immature worms were absent in the distal part of the alimentary tract. On the other hand, the differences between developing and mature worms of both sexes were not significant (females: $P = 0.67$; males: $P = 0.96$; both sexes: $P = 0.93$).

DISCUSSION

In Europe, *P. laevis* was found frequently in chub and barbel, alongside with other cyprinid fishes including minnow, and also in burbot *Lota lota* (L.), zingel *Zingel zingel* (L.) and brown trout *Salmo trutta* L. (Žitňan, 1968, 1979). Molnár (1968) reported only larval stages of *P. laevis* in minnow. It seems, therefore, that the spectrum of the preferred hosts of *P. laevis* in Central Europe may confirm this reported by Kennedy *et al.* (1989) in freshwater localities in England. Chub and barbel serve there as preferred hosts of *P. laevis*, several other cyprinid fishes and brown trout as minor hosts and a broad spectrum of other fish species as transport hosts (Kennedy *et al.*, 1989). Surprisingly, Veith & Erpelding (1995) reported *P. laevis* infection of water-living larval stages of amphibian *Salamandra salamandra* (L.) in Germany.

The Vihorlat Mountains region includes several natural lakes from which only the Great Vihorlat Lake (Morské oko) has a river output and relatively diverse fish composition (Hanzelová *et al.*, 2001). Kašťák & Žitňan, (1960) reported here *P. laevis* infections in chub, brown trout, stone loach *Barbatula barbatula* L. and minnow. Since that time, *P. laevis* prevalence and intensity of infection have decreased remarkably in all the fishes (Hanzelová *et al.*, 2001).

Within the Small Vihorlat Lake, situated about 1.5 km far from the Great Vihorlat Lake, both the minnow and *P. laevis* represented the principal dominant fish and parasite species (Dudiňák & Šnábel, 2001). *P. laevis* showed here morphological adaptations to the tiny fish host, being smaller than *P. laevis* from chub from other Slovak locality (Dudiňák & Šnábel, 2001). Regarding

the distribution of *P. laevis* in the fish and crustacean hosts, the negative binomial model fitted the present data, as usual in the majority of host-parasite systems (e.g. Crofton, 1971; Kennedy & Rumpus, 1977; Bratney, 1988). The negative binomial parameter of the aggregation of both the adult and larval *P. laevis* ranged about the upper limit of the degree ($k < 1$) found for the vast majority of macroparasitic infections of wild-life hosts and humans (Shaw & Dobson, 1995).

No significant variations have been proved in the prevalence and intensity of infection of the parasite in minnow during a year, similarly to those of *P. laevis* from dace, grayling and chub collected from river environments (Hine & Kennedy, 1974; Moravec & Scholz, 1991). Considering larval stages of *P. laevis* in *G. balcanicus*, maximum prevalence was ascertained in late summer and autumn, similarly to the data on *P. laevis* larvae in several European rivers (Van Maren, 1979; Dezfali *et al.*, 1999). The shrimp *G. balcanicus* was reported only once as a host of *P. laevis* in Ukraine (Lisitsyna & Tkach, 1996).

The proportion of males to females of both larval and adult *P. laevis* showed no significant differences from the ratio 1:1, as usual in acanthocephalans (Van Cleave, 1953; Tedla & Fernando, 1970; Muzzall, 1980; Camp & Huizinga, 1980 and many others). Despite this, the relative decrease of the male frequency occurring in winter and summer months predominantly for *Gammarus* suggests a higher sensibility of male larvae to the seasonal changes of environmental conditions for the worse (frozen or drying lake). In a lesser degree, winter and summer decrease of the adult males frequency occurred also in minnow, that has previously been observed also in *Acanthocephalus lucii* (Bratney, 1988) and *Echinorhynchus salmonis* (Tedla & Fernando, 1970), both from perch.

A detailed analysis of the changes in the rate of immature and developed acanthocephalans within both intermediate and final hosts revealed an annual life cycle previously reported in a number of heteroxenic helminths including several acanthocephalans (Walkey, 1967; Tedla & Fernando, 1970; Bratney, 1988; Molloy *et al.*, 1995). Thus, mature females producing high numbers of eggs (shelled acanthors) occurred most frequently in July (Fig. 5). Acanthellae, developing from these eggs in crustaceans, reached their frequency maximum in October (Fig. 6); then they continued in their development. Majority of them persisted in *Gammarus* as infective cystacanths during the winter, culminating in number in February. During spring months, infected crustaceans served as a source of the new-year infections of fish manifested by an increased frequency of immature worms during April and May. In the summer and autumn periods, acanthocephalans matured in fish intestine and started to produce new

dose of eggs. Therefore, a single *P. laevis* generation was evidenced per a year, although generations tended to overlap. Namely, an increased feeding activity of crustaceans together with an activation of egg output of over wintered females caused the spring rise of shrimp infections with, and a frequency of acanthellae culminated in May. Majority of larvae became infectious in July and serve as a source of throughout year infections of fish.

Some other life-cycle studies made in river environments reported irregular changes in the seasonal incidence and the developmental cycle of *P. laevis*, exhibiting both egg-producing females and new infections of fish throughout all the year (Kennedy, 1972a; Moravec & Scholz, 1991). An isolated character of the lake and specific climatic conditions can very probably alternate the life cycle processes, as mentioned also by Kennedy (1972a).

A clear preference of *P. laevis* individuals for the proximal part of the alimentary tract was noticed. Similarly, fresh-water strains of *P. laevis* from England preferred the first half of a fish intestine (Kennedy, 1972b; Kennedy *et al.*, 1976). Guillen-Hernandez & Whitfield (2001) showed two morphologically and biologically distinct strains of *P. laevis* from the flounder *Platichthys flesus* (L.) that differ in their localisation within the host gut. Thus, the fresh-water strain preferred the proximal, but the marine strain the distal parts of gut.

Immature acanthocephalans predominated in the very proximal part of the alimentary tract while developing and mature individuals were localised preferably around the first intestinal loop. As showed by Kennedy *et al.* (1976), a liberation of cystacanths from the intermediate host tissues and their activation took place within the proximal intestinal swelling of cyprinid fish, with the aid of bile components. Immature worm specimens had been then moved a further distance down the alimentary tract by peristaltic action. As parasites grow and mature, they attach to the permanent site and penetrate the wall by their proboscis and bulbs. In case of *P. laevis* and minnow, the region of the first loop represented a preferred site while the posterior third of the alimentary tract evidently provided unsuitable conditions for *P. laevis* development. No immature worms were found in this site and also older worms survived there only exceptionally.

Developing and mature worms that were permanently established in their sites, preferred the region around the first intestinal loop. Out of them, mature females and males were grouped directly in the loop. The number of mature worms decreased towards the alimentary tract more slowly than this of immature worms. In the distal portion behind the second loop, developing females and males or mature females occurred sporadically.

ACKNOWLEDGEMENTS

Authors would like to gratefully thank Assoc. Prof. Igor Hudec, Šafárik University, Košice, Slovak Republic and Assoc. Prof. Jan Helešic, Masaryk University, Brno, Czech Republic, for help with identification of crustacean intermediate hosts, Dr. Andrea Šimková, Masaryk University, Brno, Czech Republic for a translation of Summary into French and some helpful comments and L. Burik, Parasitological Institute SAS, Košice, for a technical help. Thanks are due to a staff of the Administration of the Protected Area Vihorlat and Latorica, Michalovce, the Slovak Republic for collaboration in the field research. The Slovak Grant Agency VEGA (Project No. 2/1020/21) supported this study.

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Reçu le 26 août 2002

Accepté le 5 juin 2003