ON THE HOST SPECIFICITY OF FISH TAPEWORM *PROTEOCEPHALUS EXIGUUS* LA RUE, 1911 (CESTODA)

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Summary :

Host-parasite interactions established between *Proteocephalus exiguus* and its fish hosts have been analysed in two localities in Slovakia. *P. exiguus* occurred and sexually matured in three salmonid hosts - rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta m. fario*), brook trout (*Salvelinus fontinalis*) — and in perch (*Perca fluviatilis*), first recorded as a final host of this parasite. The parasite usually strictly preferred its principal, most suitable host (rainbow trout) or some other salmonid hosts. The new fish host species (perch) harboured *P. exiguus* rather frequently, but only in altered ecosystem, if salmonids were not available in sufficient number in the environment. Large adaptive ability of *P. exiguus* manifested in its survival in four fish hosts of two distant families (Salmonidae, Percidae) and modified seasonality in unusual fish host indicate broader host specificity (stenoxenous in sense used by Euzet & Combes, 1980) than generally attributed to this species. The host specificity in some other *Proteocephalus* tapeworms is briefly discussed.

KEY WORDS : *Proteocephalus exiguus*, perch, host-parasite interactions, specificity.

Résumé : INTERACTIONS HÔTE-PARASITE DE *PROTEOCEPHALUS EXIGUUS* LA RUE, 1911 (CESTODE DE POISSONS)

Les interactions hôte-parasite établies entre *Proteocephalus exiguus* et ses hôtes poissons ont été analysées dans deux localités de Slovaquie. *P. exiguus* a été observé et a atteint le stade de maturation sexuelle chez trois salmonidés — la truite arc-en-ciel (*Oncorhynchus mykiss*), la truite saumonée (*Salmo trutta m. fario*), le saumon de fontaine (*Salvelinus fontinalis*) — et la perche (*Perca fluviatilis*), signalée pour la première fois comme hôte final du parasite. Habituellement, le parasite marque une préférence très marquée pour l'hôte principal le plus adapté (truite arc-en-ciel) ou pour d'autres espèces de salmonidés. La nouvelle espèce de poisson-hôte (la perche) abrite relativement fréquemment *P. exiguus*, mais seulement dans un écosystème modifié, si le nombre de salmonidés disponible est insuffisant. La grande capacité de *P. exiguus* à s'adapter chez quatre poissons hôtes de deux familles éloignées (Salmonidae, Percidae) et la capacité à s'adapter au cycle saisonnier d'un hôte inhabituel indiquent une spécificité de l'hôte plus large que celle généralement attribuée à cette espèce (sténoxène au sens d'Euzet et Combes, 1980). La spécificité de l'hôte de quelques autres *Proteocephalus* est brièvement discutée.

MOTS CLÉS : *Proteocephalus exiguus*, perche, interactions hôte-parasite, spécificité.

INTRODUCTION

The term « species specific » in reference to the host specificity of *Proteocephalus* cestodes parasitizing freshwater fish has been used rather loosely for many years. These parasites have generally been considered to develop to sexual maturity only in a single host species (Chubb *et al.*, 1987), in fish hosts related to one genus or exclusively to a single family (Priemer, 1982, 1987). A few experimental studies have also been done. Cross-infections yielded always negative results and thus substantiated a narrow host specificity in the final host (Willemse, 1968, 1969; Priemer, 1980).

A confidence in a strict host specificity has led to the erection of numerous spurious taxa in the genus, mainly on the grounds that the parasite was found for the first time in another host. Fifteen *Proteocephalus*

species described from salmonids and coregonids can serve as a good example (Hanzelová & Scholz, 1993; Scholz & Hanzelová, 1994; Hanzelová *et al.*, 1995a). Therefore, studies dealing with the host specificity of taxa within the genus *Proteocephalus* are not only of theoretical interest but they are also of importance in taxonomical investigations on *Proteocephalus* spp. The present study was focused on host-parasite interactions between *P. exiguus* and its fish hosts in two different localities, with an emphasis on the question of its final host specificity.

MATERIALS AND METHODS

The study was carried out in two localities in Slovakia in the period of 1993-1995 :

- 1) Morské Oko lake (locality 1) situated 48°55'N, 22°12'E, 619 m above the sea level; water surface 14 ha

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and maximum depth 25 m. Morské Oko is a little oligotrophic lake. The isolated water area emerged naturally with a Holocene volcanic landslide in the Vihorlat mountains. It is supplied by six water veins. The lake was originally inhabited by trouts. Recently, both autochthonous (*Salmo trutta* m. *fario*, *S. trutta* m. *lacustris*) and introduced (*Oncorhynchus mykiss*) trouts became to be scarce, while perch (*Perca fluviatilis*), which appeared about 1970, represents the dominant fish species in the lake (Holčík, 1969; Vološčuk & Terray, 1987).

2) Dobšiná water reservoir (locality 2) was created by damming the Hnilec river in the Slovak Ore Mountains, situated 48°52'N, 20°23'E, 786 m above the sea level; water surface 95 ha and maximum depth 22.5 m. Salmonid fish species represented by brown trout (*S. trutta* m. *fario*), rainbow trout (*O. mykiss*), brook trout (*Salvelinus fontinalis*) and grayling (*Thymallus thymallus*) are abundant in the lake. Density of perch (*Perca fluviatilis*) population is also very high.

Some cyprinids (*Abramis brama*, *Phoxinus phoxinus*, *Rutilus rutilus*, *Leuciscus cephalus*, *Noemacheilus barbatulus*, *Scardinius erythrophthalmus*) were also present in both lakes.

Cestodes were collected at all seasons of the year, mainly in the period from February to June, as then adult worms of both species are obtainable. The worms were processed by standard morphological methods and identified using discriminative criteria stated by Hanzelová *et al.* (1995b). Scanning electron microscopy in parallel with isoenzyme analysis was used to confirm the species identification based on standard

morphology. The number of 125 and 70 specimens of *P. exiguus* and *P. percae*, respectively, were analysed.

RESULTS

LOCALITY 1 : PRINCIPAL HOSTS OF *P. EXIGUUS* - SALMONIDS - WERE NOT AVAILABLE IN SUFFICIENT NUMBER IN THE LAKE

The only *Proteocephalus* species (*P. exiguus*) was found to occur in Morské Oko lake. It reached a sexual maturity in three fish hosts: rainbow trout, brown trout and perch (Table I). The most heavy infection was found in a single examined rainbow trout (55 specimens attached in pyloric caeca). The other salmonid host, brown trout, was infected rather frequently (prevalence 55.6 %), however, the mean intensity of infection was considerably lower than that in rainbow trout.

Besides salmonid hosts, *P. exiguus* matured also in perch, which is regarded as a new host of the parasite. The tapeworms occurred less frequently (prevalence 17.6 %), but regularly in perch. They were smaller in the total size, but basic morphological characters corresponded well to cestodes derived from salmonids. The scolex exhibited a large, elliptic apical sucker, neck was distinct and mostly rectangular and proglottides possessed relatively short cirrus-sac (Table II). *P. exiguus* developing in perch surprisingly showed seasonality unusual for this species, being most abundant in the early spring and absent during summer months (Table III). On the other hand, in

Parasite	<i>P. exiguus</i>				<i>P. percae</i>			
	Prevalence (%)	Intensity of infection	Total number of gravid worms	Proportion of gravid worms*	Prevalence (%)	Intensity of infection	Total number of gravid worms	Proportion of gravid worms
Morské Oko lake (locality 1)								
<i>Oncorhynchus mykiss</i>	(1/1)	55/1	30	1 : 1				
<i>Salmo trutta</i> m. <i>fario</i>	55.6 (5/9)	11.6	10	1 : 5				
<i>Perca fluviatilis</i>	17.6 (15/85)	5.3	21	1 : 4				
Dobšiná water reservoir (locality 2)								
<i>Oncorhynchus mykiss</i>	55.9 (198/354)	4.2	378	1 : 2				
<i>Salmo trutta</i> m. <i>fario</i>	20.7 (12/58)	1.9	5	1 : 6				
<i>Salvelinus fontinalis</i>	56.1 (64/114)	3.4	55	1 : 4				
<i>Perca fluviatilis</i>					31.9 (92/283)	1.7	68	1 : 2

* The approximate ratio of gravid to mature and juvenile worms.

Table I. — Infection of fish hosts in the two localities investigated.

Locality	Morské Oko lake			Dobšiná water reservoir			
Parasite	<i>P. exiguus</i>			<i>P. exiguus</i>			
Host	<i>O. mykiss</i>	<i>S. trutta m. fario</i>	<i>P. fluviatilis</i>	<i>O. mykiss</i>	<i>S. trutta m. fario</i>	<i>S. fontinalis</i>	<i>P. fluviatilis</i>
Total length of cestode (mm)	75±20.0	97±11.9	50±5.6	107±44.5	40±5.1	45±11.9	128±3.5
Diameter of apical sucker	62±16.4	68±15.7	54	66	54	47±13.8	31±4.9
Neck	distinct	distinct	distinct	distinct	distinct	distinct	indistinct
Typical shape of proglottides	elongated	rectangular	rectangular	elongated	rectangular	rectangular	wider than long
LHP/WHP	1.06±0.30	0.99±0.19	1.05±0.12	1.22±0.32	0.85±0.10	0.91±0.17	0.5±0.02
Length of cirrus-sac (LCS)	210±31.9	239±35.2	222±20.1	291±65.1	206±31.6	265±28.4	307±26.9
LCS/WHP	0.42±0.07	0.38±0.06	0.38±0.03	0.41±0.05	0.32±0.08	0.39±0.04	0.26±0.02

Measurements (mean values) in µm if otherwise stated.

Table II. — Morphometrical characters of *Proteocephalus exiguus* and *P. percae* from the two localities investigated.

	Number of fish		Number of cestodes		Prevalence (%)	Mean intensity of infection
	examined	infected	gravid	others*		
Spring	9	6	5	24	66.7	4.8
Summer	33	0	0	0	0	0
Autumn	8	1	0	1	12.5	1
Winter	35	8	16	17	22.9	4.1

* Juvenile and mature.

Table III. — Seasonality of *Proteocephalus exiguus* in the atypical host (perch) from Morské Oko lake.

brown trout, *P. exiguus* was found occurring at all seasons of the year with the highest abundance just in the summer.

LOCALITY 2 : PRINCIPAL HOSTS OF *P. EXIGUUS* - SALMONIDS - WERE PRESENT IN SUFFICIENT NUMBER IN THE WATER RESERVOIR

In the second locality investigated (Dobšiná water reservoir), the two congeners, *P. exiguus* and *P. percae* occurred sympatrically. *P. exiguus* developed to sexual maturity in three salmonid hosts: brown trout, rainbow trout and brook trout and it did not occur in perch (Table I). Infection of salmonids was unequally distributed. Rainbow trout was a host most heavily infected by large worms (Table II). Brook trout was infected with a similar prevalence; however, cestodes found in this host were smaller and proportion of gravid worms was considerably lower. Brown trout harboured the smallest portion of *P. exiguus* tapeworms. The other *Proteocephalus* species, *P. percae*, was found exclusively in perch. Electrophoretic analyses confirmed that no concurrent infection and/or introgressed individuals of *P. exiguus* and *P. percae* were observed in sympatric conditions of locality 2. Both species strictly used their obvious hosts, salmonids and perch, respectively.

DISCUSSION

P. exiguus has long been considered as a parasite of coregonids, and has been reported under this name from several species of *Coregonus* (Anikieva *et al.*, 1983; Chubb *et al.*, 1987). Under the name of *P. neglectus* it was known from brown and rainbow trouts (Moravec, 1982; Priemer, 1980, 1982; Hanzelová *et al.*, 1989, 1990; Hanzelová & Špakulová, 1992), and as *P. tumidocollis* mainly from rainbow trout in North America (Wagner, 1954; Cox & Hendrickson, 1991; Hanzelová & Scholz, 1993). Recognition of synonymies (Hanzelová *et al.*, 1995a) changed inevitably the view on the host specificity of this species. Nevertheless, the range of the hosts has henceforth covered the two related families Salmonidae and Coregonidae.

With respect to the prevalence, the mean intensity of infection, the ratio of gravid to mature and juvenile worms as well as size of the worm, as analyzed in the present study, the most suitable conditions for development and successful reproduction of the parasite provides undoubtedly rainbow trout. Accordingly, among three salmonids under consideration, rainbow trout was recognized as a preferred host of *P. exiguus*. Other two salmonid hosts (brown and brook trouts) play also an important role as substitutional hosts, especially if the preferred host species is not available in a sufficient number in the lake. It was, for instance, the case of brown trout in Morské Oko lake, after rainbow trout has become scarce.

The present study demonstrates, however, that except for salmonid hosts (rainbow trout, brown trout and brook trout), *P. exiguus* was regularly found to occur and sexually mature in an additional host, perch. This novel finding confirmed that perch, belonging to phylogenetically distant family Percidae, can in certain conditions be a regular host of *P. exiguus*. Relatively

frequent occurrence of *P. exiguus* in perch in Morské Oko lake seems to be a result of the specific ecological situation in the lake. A few years ago, dense populations of trouts were decimated and displaced by introduced and expansively reproducing perch. After then, the probability of meeting typical host (trout) was significantly limited in the environment. An important role played also was the fact that perch provided a free niche (obligate parasite of perch, *P. percae*, was absent in the locality) and evidently suitable physiological conditions for trout parasite.

Preference of perch to phylogenetically more close but, inside Euteleostei relatively isolated cyprinids (Buchmann & Pedersen, 1994), was in accordance with Kennedy's general conclusions about phylogenetical consequences of the specificity. If the parasite established new systems in a host which is regarded as an unusual one, this new host is frequently a species ecologically rather than phylogenetically related to the usual host (Kennedy, 1975).

In the second locality investigated, an essential requirement for establishment of obligate host-parasite system (hosts and parasites could frequently make contact with each other) was fulfilled and factors determining the specificity were stable. Sympatric *P. exiguus* and *P. percae* strictly preferred their typical hosts in this ecosystem.

Strong seasonality in maturation of *P. percae* in its typical host is well known (Wootton, 1974; Andersen, 1978; Chubb, 1982; Valtonen & Rintamäki, 1989), as is relative lack of seasonality in *P. exiguus* (e.g. Hanzelová *et al.*, 1990). The three salmonids harboured different generations of *P. exiguus* in both localities studied in any time of the year. However, as herein observed, the seasonality of *P. exiguus* parasitizing perch in altered ecosystem of Morské Oko lake was modified, corresponding apparently to the seasonal cycle of perch parasite, *P. percae*. This phenomenon demonstrates not only rather strong effect of physiological conditions of the new host on behaviour of the parasite but, on the other hand, a great adaptive potential of this cestode as well.

Specificity is not constant and should be considered as a dynamic phenomenon (Kennedy, 1975). *Proteocephalus* genus contains both, monospecific species as well as species with the wider range of hosts. For instance, *P. macrocephalus* and *P. osculatus* parasitize exclusively one fish host species - eel (*Anguilla anguilla*) and wels (*Silurus glanis*), respectively. Both above hosts belong to the oldest groups of teleosts, Anguilliformes and Siluriformes and, consequently present very old and close host-parasite system. *P. torulosus*, on the other hand, was recorded from many cyprinid fishes (Freze, 1965). Based on the study of Hanzelová *et al.* (1995a) and present results, *P. exi-*

guus, until lately considered being the parasite of the narrow host specificity, has also a wide spectrum of final fish hosts.

A large adaptive ability of *P. exiguus*, manifested in 1) survival in numerous hosts even of different families, 2) switching of hosts under certain environmental conditions and 3) modified seasonality, can indicate a broader host specificity (stenoxenous in sense used by Euzet & Combes, 1980) as generally attributed to *P. exiguus*. Similarly, the host specificity of other *Proteocephalus* congeners should not be considered generally, but case-by-case.

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