

Role of invasive gobies for transmission of acanthocephalans of the genus *Pomphorhynchus* in the River Rhine

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Abstract

Ponto-Caspian gobies became highly abundant in many regions outside their native distribution range (e.g. Rhine River system). In the newly invaded habitats, the parasite communities of the invasive gobies are characterized by a lower species richness compared to their native range. However, acanthocephalans of the genus *Pomphorhynchus* are highly abundant, whereas in gobies they do not become mature and mostly remain encapsulated in the abdominal cavity as preadults. Thus, gobiids could either represent a dead-end host leading to a decline of the *Pomphorhynchus* sp. population (dilution effect) or act as a paratenic host that could increase the infection pressure to the original host community (spill back). To determine the importance of gobiids for one or the other process mentioned, we conducted two infection experiments using smaller and larger individuals of the definitive host chub (*Squalius cephalus*), which were infected with preadults of *P. bosniacus* collected from the abdominal cavity of *Neogobius melanostomus*.

The results showed that preadults obtained from gobiids can develop and mature in the definitive host with mean recovery rates of 17.9 % in smaller and 27.0 % in larger chubs. No infection was observed in 38.0 % and 20.0 % for smaller and larger chubs respectively. Our study clearly demonstrated that gobies serve as a paratenic host for acanthocephalans of genus *Pomphorhynchus* and thus spill back the infection into the local fish community. However, comparisons with previous experimental studies conducted with cystacanths from intermediate gammarid hosts showed that the preadults have significantly lower recovery rates than cystacanths.

Introduction

Ponto-Caspian gobies have a high invasion potential, which allow them to spread into areas distant from their native range. In recent years, they successfully established in the Baltic, Aegean and North Sea basins (Skóra and Stolarski 1993; Kakareko et al. 2009; Mierzejewska et al. 2011; Herlevi et al. 2017) and even in the North American Great Lakes (Corkum et al. 2004; Kornis et al. 2013). After the inauguration of the Main-Danube canal in 1992 several Ponto-Caspian gobiids have already invaded the Rhine River system (Stemmer 2008; van Kessel et al. 2009; Borcharding et al. 2011; Kalchhauser et al. 2013), with the round goby *Neogobius melanostomus* and bighead goby (*Ponticola kessleri*) being the most abundant and widespread species among them (Kottelat and Freyhof 2007; Borcharding et al. 2011). Although some ecological parameters such as density, fecundity, growth, predation, and parasitism were already studied in gobies from several non-native regions of the Danube River and Rhine River (Kvach 2002; Jurajda et al. 2005; Adámek et al. 2007; L'avrinčíková and Kováč 2007; Kvach and Stepien 2008; Kováč et al. 2009; Ondračková et al. 2009; Mühlegger et al. 2010; Kalchhauser et al. 2013; David et al. 2018), their impact on species assemblages in the ecosystems throughout Europe and the River Rhine in particular still remains largely unknown. After their immigration, the free-living non-native species may harm endemic organisms and may change the species composition within ecosystems. Direct effects of introduced species on local fauna are often a result of passive or active competition for resources (space and/or food), predation, and/or hybridization with native species (Mooney and Cleland 2001; Dextrase

and Mandrak 2006; Shochat et al. 2010). Ponto-Caspian gobies for example were found to negatively affect the population densities of some native fish species (Dubs and Corkum 1996; Mooney and Cleland 2001; Balshine et al. 2005; Karlson et al. 2007; Jakšić et al. 2016; van Kessel et al. 2016). Apart of this, invasive free-living species may also indirectly influence the biodiversity by changing the composition of the parasite communities in the new area (Torchin et al. 2003; Calhoun et al. 2018; Hohenadler et al. 2019), as parasites can reduce host density (Anderson and May 1978; May and Anderson 1978; Kuris and Lafferty 1992; Hudson et al. 1998) or decrease host body size (Torchin et al. 2001). They can for example co-introduce their own endemic parasites, which can “**spill over**” to native populations (Torchin et al. 2003; Prenter et al. 2004; Kelly et al. 2009; David et al. 2018; Hohenadler et al. 2018b). Hohenadler et al. (2018a) provided examples of how the acanthocephalan *Pomphorhynchus laevis* (which, according to a recent molecular characterization should now most likely be considered as *Pomphorhynchus bosniacus*, see Reier et al., 2019), which was introduced by Ponto-Caspian invaders can outcompete a local acanthocephalan species (*Pomphorhynchus tereticollis*) and thus change the species composition of the parasite communities in the Rhine system. As the evidence for the occurrence of *P. bosniacus* in Central Europe (Reier et al. 2019) was published after the study by Hohenadler et al. (2018a), it cannot be decided with certainty in retrospect whether they found *P. laevis* or *P. bosniacus* in the Rhine system although the latter seems to be more likely.

Additionally, invasive species can contribute to the life cycle of native parasites. If an invasive species can serve as a suitable (e.g. intermediate, paratenic or final) host for local parasites, these parasites may “**spill back**” to other local hosts which will consequently increase their infection rates within the native host populations (Kelly et al. 2009; Šlapanský et al. 2016). For example, Hohenadler et al. (2018b) demonstrated that gobies in the Rhine River can contribute to the transmission of the eel swim bladder nematode *Anguillicola crassus* by serving as a paratenic host, thereby leading to higher infection levels in its definitive hosts, the European eel. In contrast, invasive species might also be responsible for a decrease of the infection risk in the native host populations (e.g. Gagne et al. 2016; Šlapanský et al. 2016). The so-called “**dilution effect**” occurs if the invaders serve as inappropriate hosts for local parasites, in which the parasites cannot develop further or if they are not favored as food item by a predatory definitive host (Ostfeld and Keesing 2000; Johnson et al. 2012).

According to previous studies more than 20 different parasite species are known to infest gobiids in the native range of their distribution (e.g. Lower Danube and Black Sea area; see Kvach 2005; Ondračková et al. 2006), while a significantly lower number of species is usually reported for non-native areas. Within the well documented and studied Rhine River for example, only eight different species have been reported for *N. melanosomus* (Emde et al. 2012, 2014; Ondračková et al. 2015) and seven for *P. kessleri* (Ondračková et al. 2015). In general, Ponto-Caspian gobies show high infestation rates with acanthocephalans of the genus *Pomphorhynchus* in both, their native and non-native range of distribution, with a prevalence often exceeding 90% and accordingly high intensities (Kvach and Skóra 2006; Francová et al. 2011; Emde et al. 2014; Ondračková et al. 2015). However, individuals of *Pomphorhynchus* sp. cannot complete their life cycle in gobies and therefore remain encysted in their abdominal cavity as larval or preadult stages. Mainly cyprinids serve as appropriate definitive hosts,

whereas in the Rhine River fish species such as barbel (*Barbus barbus*), chub (*Squalius cephalus*) or idle (*Leuciscus idus*) play the major roles (David et al. 2018; Hohenadler et al. 2018a). Therefore, until now the relevance of Ponto-Caspian gobiids for the transmission of *Pomphorhynchus* spp. remains unclear. On the one hand, they can reduce the risk of infection for the native fish populations (dilution effect) if the acanthocephalans cannot be transmitted successfully from gobiids to other fish hosts. On the other hand, the gobiids might increase the infection risk, if they serve as an appropriate paratenic host (spill back), which is preyed by local piscivorous definitive host.

The aim of this study was to understand the role of invasive gobies for the transmission of acanthocephalans from the genus *Pomphorhynchus*. In order to evaluate the infection potential of preadult (larval) stages obtained from the abdominal cavity of gobiids, a laboratory infection experiment with chub (*S. cephalus*) was performed to determine infection success (i.e. recovery rate) and development of the preadult acanthocephalans. The resulting data were compared with results from previous infection experiments in which cystacanths of *Pomphorhynchus* sp. were administered to chub.

Materials And Methods

Acanthocephalan sampling and fish infection

Infection experiments with acanthocephalans of the genus *Pomphorhynchus* were performed with chub (*S. cephalus*), as an appropriate definitive host. The fish were obtained from aquaculture facilities of the Research Institute for Nature and Forest, Belgium, where they were raised in spring water. Accordingly, they could be assumed to be free of any infections with metazoan parasites, which was verified by ten, randomly chosen chub, which were killed, dissected and screened with light microscopy for parasites.

Cysts containing preadults of *Pomphorhynchus* sp. were collected from the abdominal cavity of *N. melanostomus*. The latter were sampled by professional fishermen near Kalkar at the Lower Rhine River (844 river km) and kept alive in aerated water tanks. Prior to the infection experiments, the gobies were sacrificed, dissected and the extracted acanthocephalans were placed in physiological saline (0.9% NaCl) and stored at 5°C overnight. Most of the preadult acanthocephalans were entirely enclosed by a fibrous capsule of variable thickness (see Fig. 1). Worth noticing here is, that some thick-walled cysts were not light transparent at all and the preadults inside appeared almost completely degenerated. Therefore, such cysts with preadults were not considered for the infection experiments.

Subsequently, the cysts containing the larvae were collected randomly from a Petri-dish and were introduced to the digestive tracts of chubs by using a 2 ml syringe equipped with a 12 cm plastic tubing of 1 mm diameter (for details see Sures and Siddall, 2003). In total, 23 chubs were experimentally infected, whereas one group of fish (n = 13) was infected with six acanthocephalans per fish (1st experiment) and another group of fish (n = 10) was infected with ten acanthocephalans each (2nd experiment). As both groups were not infected at the same time (approximately six months difference) the second group of chubs (n = 13) exhibited on average a larger body size than the other (17.4 cm total

vs 11.2 cm length, respectively; see Table 1). However, chubs were from the same brood and were held under the same conditions over time. Before and after the infection, the fish were kept in 500 l tanks with dechlorinated tap water and fed twice per week with commercial pellets. A light cycle with a ratio of 16:8 (light: dark) was simulated in order to provide conditions similar to those in their natural habitats. After ten weeks the chubs were anaesthetised with 150 mg/mL MS-222 (Merck, Darmstadt, Germany) and then sacrificed by cervical dislocation. After dissection, the parasites were removed from the digestive tracts and counted. All infection experiments were carried out in accordance with the relevant guidelines and regulations and were approved by the Ethics Council (Landesamt für Natur, Umwelt und Verbraucherschutz, Nordrhein-Westfalen, permit number: 84-02.05.40.16.017).

Table 1

Morphological data of chub (*S. cephalus*) and mean recovery rates and ranges obtained for chubs infected with preadults (present study) and cystacanths of *Pomphorhynchus* sp. (see Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018)

Group	n	total length (cm)	weight (g)	condition factor	recovery of <i>Pomphorhynchus</i> sp. (%)	
		mean (\pm SD)	mean (\pm SD)	mean (\pm SD)	mean (\pm SD)	range
chub (1st experiment)	10	11.2 (\pm 0.5)	13.8 (\pm 2.4)	1.0 (\pm 0.1)	17.9 (\pm 18.6)	0–50
chub (2nd experiment)	13	17.5 (\pm 1.4)	49.4 (\pm 13.5)	1.5 (\pm 0.1)	27.0 (\pm 25.8)	0–70
Siddall & Sures (1998)	21	10.7 (\pm 7.2)	12.8 (\pm 2.8)	1.1 (\pm 0.1)	48.2 (\pm 25.0)	11–89
Sures & Siddall (1999)	20	10.7 (\pm 7.7)	13.7 (\pm 3.3)	1.1 (\pm 0.2)	44.9 (\pm 22.6)	10–78
Sures & Siddall (2003)	51	10.9 (\pm 6.9)	14.5 (\pm 3.0)	1.2 (\pm 0.1)	50.8 (\pm 24.5)	11–100
Sures et al. (2003)	36	11.3 (\pm 1.0)	10.6 (\pm 3.3)	0.8 (\pm 0.1)	70.9 (\pm 20.2)	30–100
Ruchter (2012)	55	10.9 (\pm 0.9)	9.3 (\pm 2.1)	0.8 (\pm 0.1)	58.2 (\pm 25.9)	20–100
Le et al. (2016)	14	n.a.	10.7 (\pm 2.3)	n.a.	53.6 (\pm 26.8)	0–100
Le et al. (2018)	43	11.7 (\pm 2.8)	17.1 (\pm 4.2)	0.9 (\pm 0.1)	65.1 (\pm 24.3)	0–100
n.a.: parameter is not available						

Molecular identification of parasites

As a recent study published after we performed our infection experiments indicates the presence of *Pomphorhynchus bosniacus* in major European rivers (Reier et al. 2019), we sequenced a sample of three preadults from four individual gobiids each to check the identity of the *Pomphorhynchus* species present in the investigated section of the Rhine River. The additional gobies were also sampled by professional fishermen near Kalkar at the Lower Rhine River (844 river km) three years after the infection experiment.

DNA was extracted from the preadult *Pomphorhynchus* sp. using a Chelex-protocol. Approximately 0.5 mm pieces of the parasite tissue were cut off and placed in 300 µl of a 10% Chelex 100 resin (Bio-Rad)-solution. Samples were then boiled for 20 min at 95°C and vortexed every 5 min. Subsequently, samples were cooled on ice and centrifuged at 5,000 xg for 5 min, whereas the resulting supernatant was used thereafter for PCR. The PCR was conducted with the primers PT/PL COI F and PT/PL COI R according to Tierney et al. (2020). The PCR-products were sent for sequencing (Microsynth-Seqlab) and the sequences were compared with the entries for *P. laevis* and *P. bosniacus* in the BOLD database (<https://www.boldsystems.org/index.php>).

Calculations and statistical evaluation

Fulton's condition factor (K) was calculated according to Nash et al. (2006). The recovery rates were evaluated as a percentage of the acanthocephalans recovered during dissection in relation to the number of administered preadults. In order to compare the infection success of preadult (encapsulated) *Pomphorhynchus* sp. with those of cystacanths, data from our previous infection experiments with cystacanths (Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018), were considered (for details see Table 1).

The morphological parameters of fish from the 1st and the 2nd experiment as well as the recovery rates of acanthocephalans were compared with a Mann-Whitney U-test. Kruskal-Wallis was applied for comparing the current data with studies of Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018. The recovery rates were correlated with condition factors of fish using Spearman rank correlation analysis.

Results

The subsequent molecular identification of acanthocephalans showed that all sequenced isolates were *Pomphorhynchus bosniacus* according to Reier et al. (2019), suggesting that the preadults used for the infection experiments can most likely also be classified as *P. bosniacus*.

The morphological parameters of fish used in the infection experiment are presented in Table 1. As the infection experiments were performed in different time periods, the sizes of fish individuals between both experimental groups differed significantly (cf. materials and method) with fish from the second infection experiment being significantly larger with respect to total length and body mass. However, the fish condition factor was similar during both experiments (0.97 and 0.91).

There were no significant differences between recovery rates of preadults, when comparing both infection experiments (see Fig. 2). However, the smaller chubs in the first experiment showed slightly lower mean recovery rates (17.9%) in comparison to the larger ones (27.0%) from the second experiment (Table 1, Fig. 2). The previous infection experiments with cystacanths of *Pomphorhynchus* sp. (see Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018) showed overall a significantly higher establishment of *Pomphorhynchus* sp. in the final host in comparison to the preadults used in the current study (Kruskal-Wallis test, $p < 0.05$, see Fig. 2). The lowest recovery rates for cystacanths were recovered during the infection experiment of Sures and Siddall (1999) and the highest one was obtained by Sures and Siddall (2003) being 44.8% and 70.8%, respectively (Fig. 2).

Discussion

Despite the fact that the acanthocephalans of the genus *Pomphorhynchus* occur in high prevalences and intensities in Ponto-Caspian gobies in both invasive and native distribution ranges (see Kvach and Skóra, 2006), their role for the parasite's transmission still remains unclear. Kennedy (2006) stated that acanthocephalans in accidental and paratenic hosts share the same morphological and developmental features, however, in contrast to those in accidental hosts, the acanthocephalans from a paratenic host can resume development if they are transferred to a suitable definitive host. The outcome of our infection experiment suggests that gobies such as *N. melanostomus* can serve as paratenic host for *P. bosniacus* and thus support its transfer to an appropriate definitive fish host. Given the high population density of gobies and the high infection rates with *Pomphorhynchus* spp. in newly invaded regions they can spill back the parasite and increase infection levels among the native host populations (amphipods and fish).

The involvement of paratenic hosts is common in life cycles of acanthocephalans. However, this was mostly reported for species of the classes Archiacanthocephala and Eoacanthocephala (Schmidt, 1985; summarized also by Kennedy, 2006). Among the Palaeacanthocephala, to which species of the genus *Pomphorhynchus* belong, only two genera have been reported so far (i.e. *Corynosoma*, *Leptorhynchoides*) that use paratenic hosts in order to bridge the gap between intermediate and definitive hosts. These acanthocephalans require mostly a piscivorous definitive host that do not regularly feed on crustaceans. Even if this is not the case with the species of the genus *Pomphorhynchus*, our study demonstrates that *P. bosniacus* can also use the alternative transmission route via a paratenic host. Suitable definitive host for acanthocephalans of the genus *Pomphorhynchus* in the investigated section of the Rhine River are mostly cyprinids such as chub (*S. cephalus*), common barbel (*Barbus barbus*) and idle (*Leuciscus idus*). Small fish might become one of the most important food items in the diet of large chubs or common barbel (Bašić et al. 2014; personal observation (unpublished data); see also Kottelat and Freyhof, 2007). Therefore, it can be assumed that after their establishment in newly invaded habitats the gobies might become an essential part of the diet of piscivorous and probably some omnivorous fish species, as reported for pikeperch from the newly colonized Kiel Canal (Thiel et al. 2014) or for pikeperch and perch from western Baltic Sea (Oesterwind et al. 2017). Thus, gobies are most probably also preyed as food source by different large cyprinids and might enhance the transmission of *Pomphorhynchus* species in their area of distribution.

Adults of *Pomphorhynchus* that are established in the intestine of a suitable fish definitive host can survive the predation of their fish host and even establish in the intestine of the predator. For example Kennedy (1999) investigated such a postcycling transmission of *P. laevis* by demonstrating the transfer of specimens from one definitive host to another. As the acanthocephalan's proboscis and bulb is commonly surrounded by fibrous tissue in the gut and body cavity of the definitive host, only non-mature adults can survive the transfer and continue to mature and reproduce in the new fish host. The proboscis and bulb of preadults obtained from the body cavity of gobiids were not encapsulated and remained intact, thereby being able to be used for establishment in the gut of an appropriate definitive host. However, most individuals were surrounded entirely by a fibrous capsule with a variable thickness, whereas the preadults in the thick-walled cysts appeared less vital than the others with thin-walled, or without any cyst (personal observation). Longer periods in the body cavity of the gobies probably reduce the fitness of the acanthocephalans, finally leading to an inactivation (reduced infectiveness) and death. In some cases, the parasites inside the thick-walled cysts appeared almost completely degenerated, which presumably was the result from the interaction with the host immune system. Similarly to the observations of Kennedy (1999), the preadult acanthocephalans in gobies can remain infectious probably only for a short period before they are surrounded with thick fibrous layer and thus become weakened/inactivated. Furthermore, Dezfuli et al. (2011) studied the fate of extraintestinal immature *Pomphorhynchus* sp. (preadults) encapsulated in the mesenteries and peritoneum of small sheatfish (*Silurus glanis*) that appeared to be similar to the ones found in gobiids. They found that the cyst wall consisted of two distinct layers with an outer one containing collagen fibers infiltrated with mast cells and an inner one, which was in direct contact with the parasite's tegument and comprised a large number of mast cells. Some of the latter were even located directly on the acanthocephalan tegument. As the mast cells were found to be the most common immune cells at attachment sites of *Pomphorhynchus* sp. and in the cyst wall of the extraintestinal preadults (Dezfuli et al. 2011) it can be assumed that they are responsible for the inactivation and destruction of parasites as suggested by Murray et al. (2007). Therefore, depending on the duration of the interaction between the parasites and the fish immune system, the acanthocephalans in gobies and other paratenic hosts can exhibit different fitness and capability to infect further fish hosts after predation. This would also explain the differences between the recovery rates of acanthocephalans obtained from the gobies and those taken directly from the crustacean intermediate host observed in the previous infection experiments (Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018). The vitality and infectiveness of the cystacanths in amphipods appears to be less affected over time, due to the lower complexity of the invertebrate immune response (e.g. Dezfuli et al., 1992, 2008) in comparison to those of vertebrates (e.g. for fish Dezfuli et al., 2011) as well as the immune depression induced by cystacanths in their amphipod host (Cornet et al. 2009).

Conclusions

The outcome of this study reveal that invasive gobies might serve as an appropriate paratenic host for acanthocephalans of the genus *Pomphorhynchus*. Accordingly, they can intensify the transmission of *P.*

bosniacus leading to a spill back to the local hosts in newly invaded habitats. As no coinfection with other closely related species such as *P. tereticollis* was recorded in the gobies in the present study, the role of gobiids for the transmission of other species from the genus needs to be elucidated. This might shed a light on interspecific competition between the species within the *Pomphorhynchus* genus occurring in the Rhine River system and thus reveal one of the mechanisms how *P. tereticollis* was outcompeted over time, as suggested by Hohenadler et al. (2018b).

Declarations

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Milen Nachev, Michael Hohenadler, Nicklas Bröckers, Daniel Grabner and Bernd Sures. The first draft of the manuscript was written by Milen Nachev and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript

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Figures

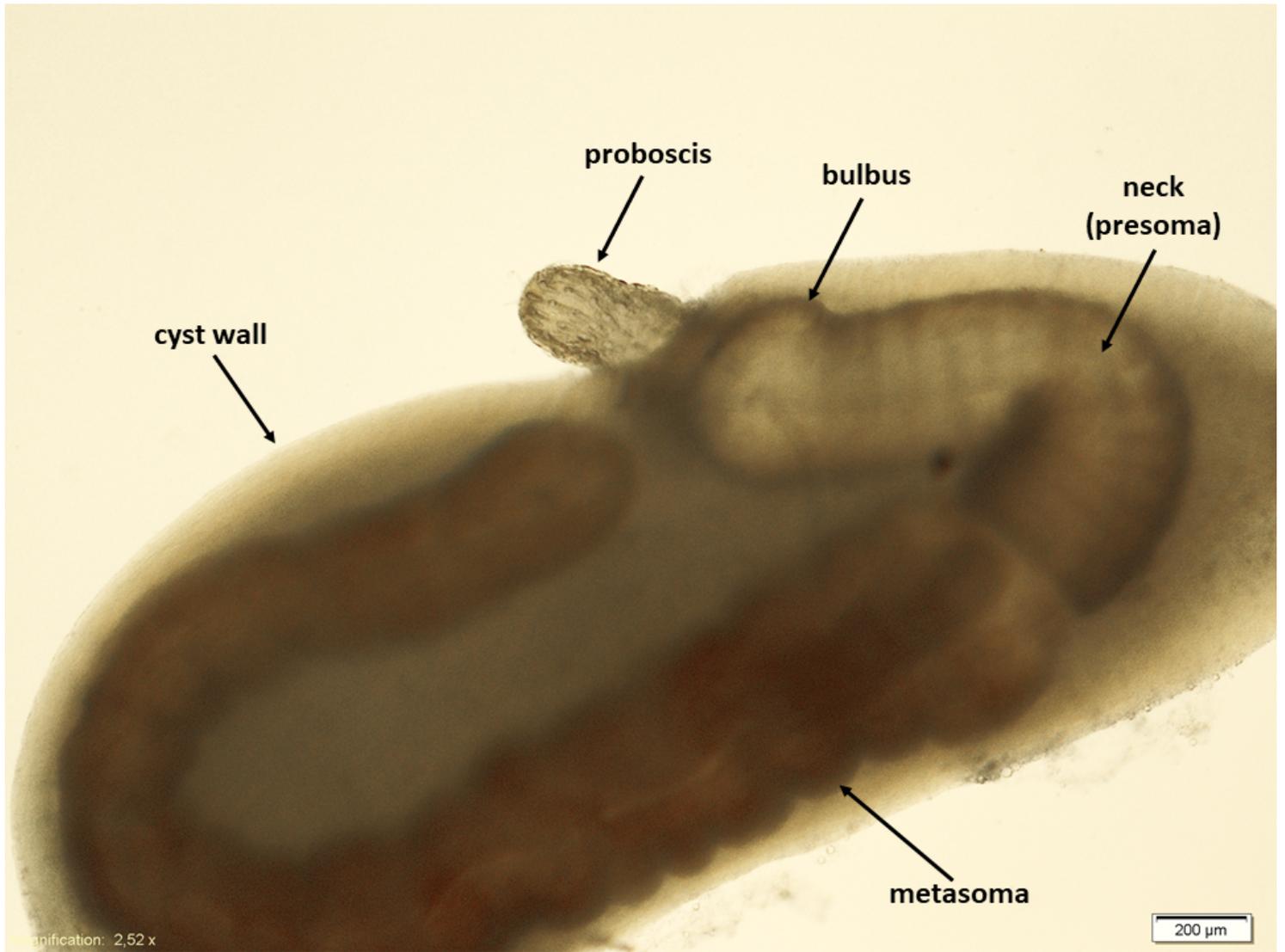


Figure 1

General occurrence of preadult *Pomphorhynchus* sp. obtained from the abdominal cavity of gobiids.

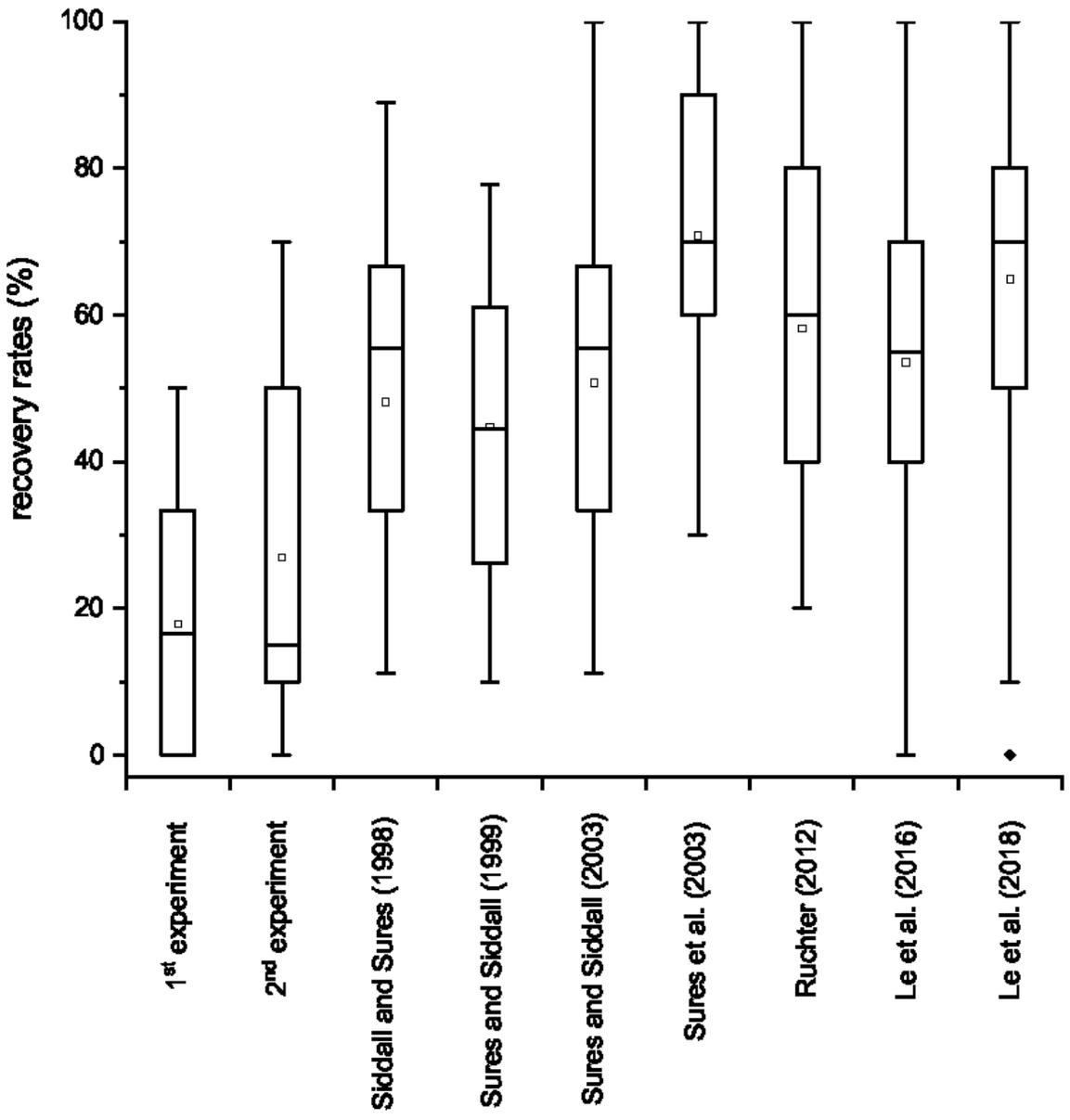


Figure 2

Recovery rates of preadults (current study – 1st and 2nd experiments) and cystacanths of *Pomphorhynchus* sp. (Siddall and Sures 1998; Sures and Siddall 1999, 2003; Sures et al. 2003; Ruchter 2012; Le et al. 2016, 2018). Open dots are means, lines within the box are medians, boxes are interquartile ranges, error bars are interdecile ranges and closed dots are outliers.