Parasitol Res (2014) 113:113–120
DOI 10.1007/s00436-013-3633-7

ORIGINAL PAPER

Temporal and spatial changes in the composition and structure of helminth component communities in European eels *Anguilla anguilla* in an Adriatic coastal lagoon and some freshwaters in Italy

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Received: 16 May 2013 / Accepted: 1 October 2013 / Published online: 18 October 2013

Abstract The composition and diversity of the helminth component communities in eels *Anguilla anguilla* were determined in three separate localities in Italy: an Adriatic coastal lagoon, Comacchio and two freshwater localities, the River Po and the Lake Piediluco. Data from Comacchio lagoon were analysed over 15 years to determine whether community composition and diversity changed significantly overtime. The community was species rich (nine species, all marine except *Proteocephalus macrocephalus*) and was dominated by a suite of digeneans: *Deropristis inflata*, *Helicometra fasciata*, *Lecithochirium musculus* and *Bucephalus anguillae*. The community showed little change in composition over the period, but the relative abundance and dominance of the species did alter. By contrast, the component communities in the freshwater localities were species poor and the dominant species were freshwater acanthocephalans, *Pomphorhyncus laevis* in River Po and *Acanthocephalus rhinensis* in Lake Piediluco. The helminth community of Lake Piediluco with five species was richer than that of the River Po with only three species, but was poorer than that of Comacchio lagoons. Similarity indices between samples from Comacchio were high; between the lagoon and the freshwater localities and between the two freshwater localities, similarity indices were very low. Helminth component community structure in coastal lagoons was comparable across Europe. The helminth community in the River Po was similar to those in the River Tiber and other European rivers whilst that in Lake Piediluco was similar to that in other European lakes. Levels of the pathogenic *Anguillicoloides crassus* in swim bladders were consistently lower in prevalence and abundance in the coastal lagoons than in freshwater localities. This suggests that this parasite may have little impact on migrating eels if they are indeed primarily of marine origin and so it may be of little importance in the recent decline of eel populations throughout Europe.

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Introduction

The recent severe declines in the populations of the European eel *Anguilla anguilla* throughout Europe (EC 2007) has stimulated interest in the possible role of parasites in this process. Much of this interest has centred on the introduced nematode *Anguillicoloides crassus* as its appearance and spread in Europe was contemporary with the eel decline and it is known to be pathogenic (Sures and Knopf 2004; Kennedy 2007). However, there have also been a number of other and more general studies on the helminth parasite communities of eels including those of Kennedy (1993), Sures et al. (1999), Norton et al. (2003), Schabuss et al. (2005) and Sasal et al. (2008) that have focused on the composition and spatial and temporal changes in the helminth fauna. The great majority of these have been on rivers and freshwater lakes of Northern Europe and only a few have extended into estuaries and the Baltic Sea and adjacent lagoons (Seyda 1973; Køie 1988a;

Orecka-Grabda and Wierzbicka 1994; Reimer et al. 1994; Jakob et al. 2008).

Whilst there have been some studies on eel parasites in the rivers of Southern Europe (Saraiva and Eiras 1996; Kennedy et al. 1998; Saraiva et al. 2005; Hermida et al. 2008) the lagoons around the Mediterranean coasts have been rather neglected. This is surprising in that they are often the sites of major commercial eel fisheries. Recently, a paper by Filippi et al. (2013) describes the occurrence of macroparasites in eels from two coastal lagoons of Corsica (France) and the influence of site, season, silvering stage and host length on the parasites communities. Some other investigations have been conducted in France and Italy (Kennedy et al. 1997; Di Cave et al. 2001), and these have indicated that the parasite communities differ considerably from those in freshwaters. The recent suggestion by Tsukamoto et al. (1998) and subsequent confirmatory studies, e.g. Daverat et al. (2004) that populations of eels from marine localities contribute primarily to future recruitment of eel populations should serve to focus more attention on the parasites of eels in lagoons of raised salinity. In Italy, there is an extensive series of such lagoons on both Tyrrhenian and Adriatic coasts. Studies on these, to date, have focused on the lagoons on the west coast near to Rome (Kennedy et al. 1997) and on a group of lagoons on the east coast near to Venice (Di Cave et al. 2001). Included in this latter group is the Comacchio lagoons, which has a long history of eel culture and is one of the most important eel fisheries on the Mediterranean coast. Despite these studies, there are still gaps in the knowledge and understanding of the eel parasites communities. In particular, it is not known how stable these communities in lagoons are over time or how similar they are to communities in freshwater lakes in Italy or to any Italian river other than the Tiber (Kennedy et al. 1998).

The aims of the present investigation are to fill in some of these gaps. The principal focus is on the Comacchio lagoons, for which there are now data on eel parasite communities over a period of 15 years. These data are then compared with data from a survey of a freshwater lake, a habitat not previously studied in respect of its eel parasites in Italy. The data are also compared with those from a survey of eel parasites in the River Po to enable a comparison to be made with the River Tiber for which there is a data set over 16 years. Ultimately, this should contribute to a more extensive picture of eel parasite communities in saline Mediterranean lagoons and their similarity to such communities in freshwater localities.

Materials and methods

Comacchio lagoons

The Po Delta Park Administration from the Comacchio Lagoons (Northern Adriatic Sea, Italy), on 10 occasions from October 2005 to May 2006, obtained 140 eels (24 yellow and 116 silver) measuring 28–92 cm in total length (70.9±14.7 cm (mean ± SD)). From March 2010 to December 2012, 46 silver eels measuring 50–93.5 cm in total length (78.0±9.6 cm) and 74 yellow eels measuring 24.5–75 cm in total length (50.2±11.9 (mean+SD)cm) were sampled from the same site in the Comacchio Lagoon. Fish were brought liver to the laboratory of the Department of Life Sciences and Biotechnology, University of Ferrara, anesthetised with MS 222 (Sandoz) and killed by severing the spinal cord. The digestive tract and associated organs were removed and the intestine cut open longitudinally and searched for helminths. The swim bladder was searched for adult nematodes.

Po river

A total of 25 yellow eels measuring 33.5–75 in total length (53.6±10.8 cm) were provided on five occasions from 2010 to 2012 by professional fishermen belonging to the Po River Consortium (Restrict of Ferrara, North Italy) using fyke nets. Fish were brought live to the laboratory of the Department of Life Sciences and Biotechnology, University of Ferrara, anaesthetised with MS222 (Sandoz) and then treated as mentioned above.

Piediluco lake

A total of 97 eels measuring 54.5±11.3 cm (mean ± SD) in total length (range, 31–76.5 cm) were sampled over five visits (May and October 2010, April and July 2011 and May 2012) from Lake Piediluco (Umbria Region, Centre of Italy) by professional fishermen belonging to the Piediluco Fish Consortium using fyke nets. Immediately upon landing, the fish were removed and transferred alive to the Consortium's facility where they were euthanized using an overdose of MS222. Thereafter, the spinal cord was severed and the fish weighed and measured. Postmortem, the digestive tract of fish was removed and searched longitudinally for parasites as was the swim bladder.

As the aims of the investigation were to compare helminth parasite communities in time and space, all comparisons were carried out at the component community (*sensu* Holmes and Price (1986) and as defined by Bush et al. (1997)) level only. The measures of community structure and similarity adopted were those used in studies of helminth communities of eels from Adriatic lagoons (Di Cave et al. 2001) to facilitate comparisons. Prevalence and abundance were used as defined by Bush et al. (1997). The measures of community structure adopted were species richness, the Shannon–Weiner Index and its Evenness and the Berger–Parker Dominance Index. Similarities were measured using Sorensen's index and the percent Similarity Index. All parameters were calculated as defined by Magurran (1988), using natural (ln) logs when appropriate. All analyses were carried out on the entire samples of eels regardless of their size, but yellow and silver eels were analysed separately in the later samples from Comacchio Lagoon.

For scanning electron microscopy (SEM) some specimens of different parasite species were fixed and processed according to the methods described in detail in Dezfuli et al. (2012).

Results

Temporal changes in helminth community structure

The changes in the composition of the helminth community in eels in Comacchio over 15 years are shown in Table 1. The community is composed of nine species in total, *Deropristis inflata* (Fig. 1a), *Bucephalus anguillae* (Fig. 1b), *Lecithochirium musculus*, *Tetraphyllidea* (Fig. 1c), *Contracaecum rudolphii* (Fig. 1d), *Proteocephalus macrocephalus*, *Cosmocephalus obvelatus*, *A. crassus* and *Helicometra fasciata* (Fig. 2a), with a maximum of eight in yellow eels in 2012. All the species except *P. macrocephalus* are marine. *A. crassus* is generally considered to be a freshwater species, but it is able to survive raised salinity and even fully marine conditions. There is a suite of common species that are all marine digeneans. The identity of the species in this cluster has not changed over the period, but their abundance, both relative and absolute, has. In 1997, *D. inflata*, *H. fasciata* and *L. musculus* exhibited similar high values of prevalence, but *D. inflata* was the most abundant species and *L. musculus* the least. By 2005–2006, *B. anguillae* had increased in prevalence and it remained at a high level of both prevalence and abundance thereafter. Over the same period, *H. fasciata* declined in prevalence but not abundance, whereas *D. inflata* declined in prevalence from 1997 to 2005–2006 but not thereafter although abundance declined steeply to 2005–2006 and remained at a very low level. Over the same period, *L. musculus* declined in prevalence and abundance. By contrast, *Contracaecum* larvae increased in prevalence over the same period and to some extent in abundance. The prevalence of *A. crassus* declined over the period of investigation as did its abundance, but to a lesser extent. The presence of *P. macrocephalus* in one of the samples suggests that an eel has moved into a less saline part of the lagoon at some point. Thus, the composition of the helminth fauna remained relatively unchanged over the period of study, but the proportions of each species did not even though the suite of digenean species remained the commonest component of the community.

These changes are summarised more clearly in Table 2. The Berger–Parker Dominance Index was highest in 1997 and 2010, but the dominant species was always a digenean: at first, *D. inflata* (Fig. 1a) and then *H. fasciata* (Fig. 2a). The Shannon–Weiner Index rose from 1997 to 2005–2006, and then remained high despite some variation. This again confirms that even though composition of the community remained constant, the relative abundance of the species changed over time.

Differences in the composition and relative abundance of helminth species between yellow and silver eels could only be tested in 2010/2012, when they were clearly very slight as far as the intestinal species were concerned. Larval species

Table 1 Selected characteristics of the helminth fauna of all eels from the Comacchio lagoons

Year	1997			2005–2006			2010–2012					
Status of eel	Yellow			Yellow and Silver			Yellow			Silver		
No. of eels	42			140			74			46		
Parasites	Prevalence	A	SD	Prevalence	A	SD	Prevalence	A	SD	Prevalence	A	SD
Bucephalus anguillae	2.4	0.1	(0)	49.9	3.7	(11.8)	45.9	3.8	(8.6)	47.8	9.2	(22.2)
Deropristis inflata	73.8	29.7	(67)	36.4	2.3	(78)	28.4	1.8	(3.8)	30.4	3.5	(10.3)
Helicometra fasciata	73.8	13.8	(21.7)	59.3	9.6	(25.3)	59.5	14.2	(31.1)	52.2	16.8	(51.1)
Lecithochirium musculus	69.0	2.3	(6.6)	9.3	1.3	(5.7)	13.5	0.9	(2.9)	15.2	1.7	(5.5)
Tetraphyllidea (l)	0			16.4	0.7	3.1	2.7	0.14	0.9	15.2	1.1	3.2
Proteocephalus macrocephalus	0			0			4.1	0.2	0.9	0		
Contracaecum rudolphii (l)	9.5	0.2	15.0	24.3	2.9	7.2	17.6	1.1	2.7	32.6	4.1	8.1
Cosmocephalus obvelatus (l)	4.8	0.1	0	0			0			0		
Anguillicoloides crassus	11.9	0.1	0.4	2.1	0.04	0.3	6.8	0.1	0.5	4.3	0.04	0.2

The 1997 data is from Di Cave et al. (2001). In this paper, *Bucephalus anguillae* was originally considered to be *B. polymorphus* but was subsequently (Spakulova et al. 2002) recognised as a new species

A abundance, *SD* standard deviation of abundance, *l* larval form

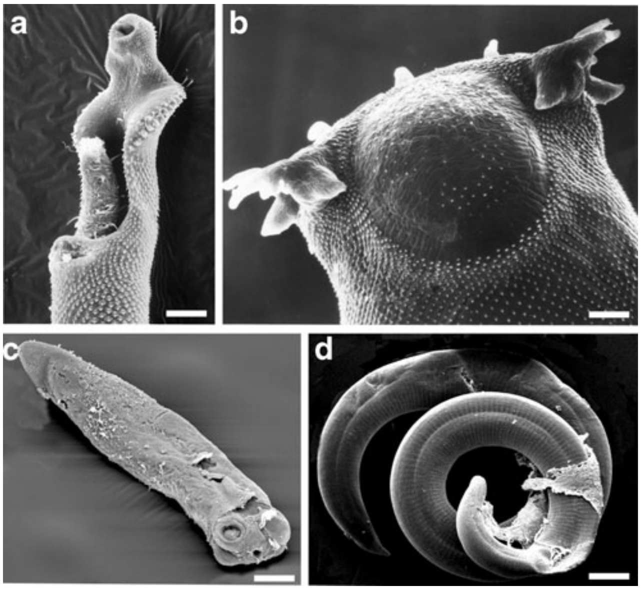

Fig. 1 Scanning electron microscopy micrographs of parasites of *Anguilla anguilla* from Comacchio lagoons. **a** *Deropristis inflata*, anterior part, *scale bar* 97 μm. **b** High magnification of apical region of *Bucephalus anguillae*, *scale bar* 26 μm. **c** *Tetraphyllidea* larva, *scale bar* 120 μm. **d** *Contracaecum rudolphii* larva, *scale bar* 143 μm

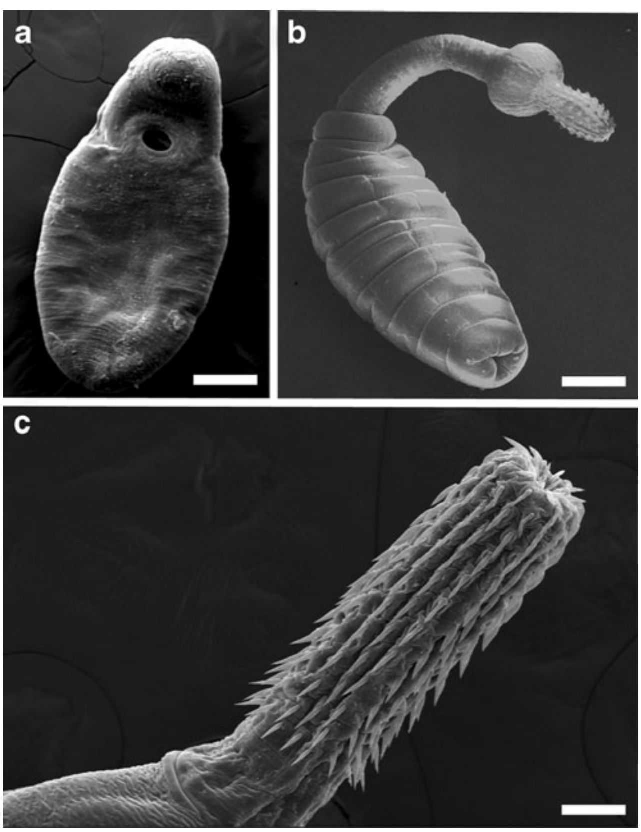

Fig. 2 Scanning electron microscopy micrographs of dominant species in three separate localities. **a** *Helicometra fasciata* in eels from Comacchio lagoons, *scale bar* 230 μm. **b** *Pomphorhynchus laevis* in *A. anguilla* from River Po, *scale bar* 350 μm. **c** *Acanthocephalus rhinensis* in eels from Lake Piediluco, *bar* 85 μm

increased in abundance with eel age, as would be predicted. These findings justify not separating yellow and silver eels in the other samples.

Spatial changes in helminth community structure

The helminth communities in the River Po and Lake Piediluco are shown in Table 3. The intestinal community in the River Po is clearly species poor, with only two species, and these are both freshwater species. Species diversity is low (Table 2), but the dominance index is high (0.87) and the intestinal community is dominated by the acanthocephalan *Pomphorhyncus laevis* (Fig. 2b). The most prevalent and abundant species in the river is the swimbladder nematode *A. crassus*. Both prevalence and abundance of *A. crassus* are higher than in the saline lagoons of Comacchio (28.0 vs. 11.9 % and 1.12 vs. 0.1 max).

The helminth community of Lake Piediluco with five species (Table 3) is richer than that of the River Po, but is still poorer than that of Comacchio lagoons. All the species are again freshwater in origin. Species diversity is low and the dominance index is high at 0.89 (Table 2). The dominant species is again an acanthocephalan, in this locality *Acanthocephalus rhinensis* (Fig. 2c). Once again, *A. crassus* is present at higher levels than in Comacchio lagoon with a prevalence of 20.6 % and an abundance of 0.8 (Table 3).

The differences between the helminth communities of the freshwater and marine localities are also evidenced by the similarity indices (Table 4). The Comacchio samples exhibit a very high degree of similarity (Sorensen's index, 0.77–0.92) and a somewhat lower level of percent similarity index (41.8–69.9). Not surprisingly, the highest levels of similarity were found between the 2005–2006 and 2010–2002 samples, i.e. the two most recent ones. By contrast, the similarity levels between the lagoon and the freshwater localities are very low (less than 0.01 for the percentage similarity and less than 0.25 for Sorenson's index). Even the similarity indices between the two freshwater sites are very low. These findings support the view that the intestinal parasite communities of Comacchio lagoon were fairly similar in composition and structure over the 15-year period of study, but they differ strongly from the intestinal helminth communities of the two freshwater localities. These latter communities are similar only in that they are species poor and each is dominated by acanthocephalan species. The greatest similarity between them comes from the high prevalence levels of *A. crassus*.

Discussion

There are few long-term datasets on helminth parasite communities in eels with which the present data from the Comacchio lagoons can be compared, and none of these sets are from coastal lagoons. The previous studies on eel parasite

Table 2 Diversity characteristics of the intestinal helminth communities from the Comacchio lagoons and the River Po and Lake Piediluco

Locality	Comacchio				River Po	Lake Piediluco
Year	1997	2005–2006	2010–2012		2010–2012	2010–2012
Status of eels	Yellow	Yellow and Silver	Yellow	Silver	Yellow	Yellow and Silver
No. of eels	42	140	74	46	25	97
No. of helminth species	6	6	7	6	2	4
Shannon–Weiner Index	0.85	1.46	1.14	1.37	0.37	0.40
S–W evenness	0.44	0.75	0.55	0.70	0.54	0.28
Berger–Parker Index	0.64	0.46	0.64	0.46	0.87	0.89
Dominant species	*Deropristis inflata*	*Helicometra fasciata*	*Helicometra fasciata*	*Helicometra fasciata*	*Pomphorhynchus laevis*	*Acanthocephalus rhinensis*

communities in Italian lagoons (Kennedy et al. 1997; Di Cave et al. 2001) report findings from one moment in time only. Studies on Corsican lagoons (Caillot et al. 1999; Ternengo et al. 2005) also report on data from one sample only. The only long-term data on helminth communities in eels in Italy are from the River Tiber (Kennedy et al. 1998). These described changes similar to those in Comacchio in that community richness and diversity did not change significantly over 16 years. There were changes in community composition but the same species remain dominant throughout the period.

Other long-term studies are from freshwater localities throughout Europe and they do not report consistent findings. Long-term data on eel parasite communities in small rivers in England (Kennedy 1993, 1997) reveal large changes in composition, structure and dominance in the communities. These, however, may reflect physical changes in the habitats themselves brought about by bank strengthening and flood relief schemes. By contrast, the parasite communities in eels in the River Shannon (Lough Derg) in Ireland showed considerable stability in composition, structure and dominance over a period of 18 years (Kennedy and Moriarty 2002). A more complicated situation was revealed in Lake Neusiedler See in Austria by Schabuss et al. (2005). The helminth community of eels was species poor, but in the north basin the dominant species changed over the 8-year period of study although the community structure remained similar. In the south basin, by contrast, dominance and composition remained more or less constant over the same period. It can only be concluded therefore, that the helminth intestinal communities in eels in coastal lagoons can show stability in composition and structure even if there are changes in dominance and species abundance. Given the absence of comparable long-term studies from other coastal lagoons and the variety of findings from freshwater habitats, it is impossible to know how widespread the pattern found in Comacchio may be.

Much of the stability in Comacchio appeared to relate to the fact that the community was dominated by a suite of marine digeneans, two species of which, *D. inflata* and *L. musculus*, can be considered eel specialists whereas the others are generalists. Other helminth species are present in small numbers, but most make little contribution to community structuring. The relative abundance of individual species in

Table 3 Selected characteristics of the helminth fauna of freshwater localities

Locality	River Po			Lake Piediluco		
Year	2010–2012			2010–2012		
Status of eels	Yellow			Yellow and Silver		
No. of eels	25			97		
Parasites	Prevalence	A	SD	Prevalence	A	SD
Proteocephalus macrocephalus	4.0	0.04	0.20	6.2	0.2	0.8
Dentitruncus truttae	0			20.6	1.5	4.0
Acanthocephalus rhinensis	0			61.9	16.2	40.6
Pomphorhyncus laevis	8.0	0.28	0.98	0		
Raphidascaris acus	0			5.2	2.1	0.6
Anguillicoloides crassus	28.0	1.12	2.39	20.6	0.8	1.8

A abundance, *SD* standard deviation of abundance

Table 4 Indices of similarity between intestinal helminth component communities of localities sampled

Locality	Comacchio 1997 vs. 2005–2006	Comacchio 1997 vs. 2010–2012	Comacchio 2005–2006 vs. 2010–2012	Comacchio vs. Piediluco	Comacchio vs. Po	Piediluco vs. Po
Percent similarity index	41.8	44.9	69.9	<0.01	<0.01	<0.01
Sorensen's index	0.83	0.77	0.92	0.18	0.22	0.33

All comparisons with Comacchio 2010–2012 data for yellow eels

the suite, and hence of dominance, can change over time, but this had little impact on the overall structure of the community. This may be a general characteristic of eel helminth communities in coastal lagoons. A similar suite of digeneans dominated the intestinal helminth communities of eels in other Adriatic lagoons (Di Cave et al. 2001) and in Tyrrhenian coastal lagoons (Kennedy et al. 1997). The levels of similarity in the helminth component communities of all these lagoons were fairly high (Di Cave et al. 2001).

In fact, eel intestinal helminth communities from waters of enhanced salinity, whether estuaries, lagoons or the Baltic Sea show similarities brought about by this suite of digeneans. In Iceland, four marine digenean species dominated the communities (Kristmundsson and Helgason 2007), the only other species being the eel specialists *Bothriocephalus claviceps* and *P. macrocephalus*. This latter species was also found in Comacchio and other Italian lagoons. In Portugal, Hermida et al. (2008) recognised two suites of helminths in the eel parasite communities in the brackish water lagoon in the estuary of the Rio de Alveiro: a digenean suite of marine species including *D. inflata*, *Lecithochirium rufoviride*, *H. fasciata* and *Podocotyle* sp. and a more freshwater suite of *P. macrocephalus* and two freshwater species of acanthocephalans. The dominant species was *D. inflata*. Maillo et al. (2005) found the same digenean suite in coastal lagoons of the Ebro delta. Even in the Corsican Urbino lagoon, *D. inflata* and *L. musculus* were the core species, with *D. inflata* dominant (Ternengo et al. 2005). Similarly in the Baltic Sea, Køie (1988a) and, later, Jakob et al. (2008) identified this suite of digeneans dominating eel helminth communities. In another lagoon of Corsica (Biguglia lagoon), characterised by a lower salinity, the digenean species *B. anguillae* and *L. musculus* were absent, whilst *P. macrocephalus*, *Pseudodactylogyrus anguillae* and *Ergasilus gibbus* showed high occurrence and/or abundance (Filippi et al. 2013). Eels in lagoons may also harbour mixed communities: Bystydzieńska et al. (2005) described the eel community in a Vistula lagoon as comprising *D. inflata* and *Brachyphallus crenatus* (marine), *B. claviceps* and *P. macrocephalus* (freshwater but tolerant of low salinities) and the acanthocephalans *Echinorhynchus gadi* (marine) and *A. anguillae* and *A. lucii* (freshwater). It is interesting to note, in Corsican lagoons, the absence of *H. fasciata* (Ternengo et al. 2005; Filippi et al. 2013) which is the dominant species in Comacchio lagoon after 2005.

As estuaries and rivers become less saline, so the eel helminth community changes. In the present study, communities in Lake Piediluco and the River Po were similar only in that they were species poor, with low diversity and high dominance. Both were dominated by a species of acanthocephalan. The River Po was dominated by *P. laevis*, Lake Piediluco by *A. rhinensis* (Dezfuli et al. 2012) and the River Tiber by *A. clavula* (Kennedy et al. 1998). Acanthocephalans are rarely found in eels in lagoons (Filippi et al. 2013), but are frequently found dominating helminth communities in freshwaters. Both lakes (Schabuss et al. 2005) and large rivers including the Rhine (Sures et al. 1999; Amin et al. 2008), the Thames (Norton et al. 2003, 2004) and the Shannon (Kennedy and Moriarty 2002) are dominated by acanthocephalans in the freshwater reaches, but acanthocephalan abundance declines as rivers near their estuaries. Small rivers are less predictable as communities are often species poor (Kennedy 1993, 1997; Borgsteede et al. 1999): diversity may be low, but dominance may be high or low and by an acanthocephalan or a nematode as in tributaries of the River Exe (Kennedy 2001). Digeneans are sometimes present in freshwater communities, but are seldom common (Køie 1988b) and only exceptionally dominate (one locality in the River Thames at Windsor: Norton et al. 2003). In the lower reaches of a river, *D. inflata* may be present in low numbers (Kennedy 1993, 1997; Orecka-Grabda and Wierzbicka 1994). As Jakob et al. (2008) have demonstrated and expressed so neatly, the Baltic Sea integrates freshwater and marine helminth communities in eels, given that species show salinity dependent specificities, but low diversity and high dominance are common in most habitats.

Although *A. crassus* was not strictly part of the aims of the present investigation, the opportunity to obtain further information on its infection levels, particularly in coastal lagoons, was taken in view of its pathological importance and possible role in the decline in eel populations. Its prevalence and abundance remained low throughout the period of the investigation in Comacchio, and indeed it could be considered that it had decline slightly since 1997 (Table 1). By contrast, both parameters were much higher in the freshwater localities. It was not found in any of the more saline Tyrrhenian lagoons (Kennedy et al. 1997) which may simply reflect the fact that it had not yet invaded them, but it was found in the least saline lagoon Burano. Di Cave et al. (2001) found it in the lagoon

Figheri at similar levels to those in Comacchio. By contrast, it was found in both freshwater localities in the present study at levels comparable to, but lower than in the River Tiber (Kennedy et al. 1998).

A. crassus has been reported from the Baltic Sea (Reimer et al. 1994) and from estuaries in brackish water (Pilcher and Moore 1993). It was also found in Corsican lagoons at similar levels (13 % prevalence and 0.16 abundance) to those in Comacchio (Caillot et al. 1999; Ternengo et al. 2005). The parasite can survive and reproduce in eels in 50 and 100 % sea water for at least 6 months and so it has the ability to infect eels in the Baltic, in estuaries and in coastal lagoons (Kirk et al. 2000a, b). However, hatching rate, larval survival and the period of infectivity decline with salinity (Kirk et al. 2000b, 2002), may explain the lower infection levels in lagoons. It can nevertheless be carried to sea with silver eels migrating from the lagoons.

There is general agreement (summarised in Kennedy 2007) that *A. crassus* has deleterious effects upon its eel host and that it can be considered a serious pathogen of eels at high abundance levels. Apart from histopathological damage to the swim bladder (Knopf et al. 2008), it can reduce the ability of the swim bladder to function as a hydrostatic organ during migration (Lefebvre et al. 2011). It can also impair the swimming performance of infected eels and trial simulations confirmed that eels with high levels of infection could show migration failure (Palstra et al. 2007; Lefebvre et al. 2011). However, Tsukamoto et al. (1998) have suggested that the spawning population of eels derives only from marine populations present in coastal lagoons and estuaries (see Daverat et al. 2004). If this is the case, the high levels of infection encountered in freshwaters may be of little or no importance in respect of eel migration successes. If levels of *A. crassus* in marine eels are as low as those found in the Italian and Corsican coastal lagoons, and this does seem to be the case, then this would suggest that *A. crassus* infections may be of little or no importance in the recent decline of eel populations throughout Europe.

Acknowledgments Thanks are due to F. Bisonni from the Fisheries Consortium of the Lake Piediluco and to the professional fishermen of Ferrara R. Boschetti and C. Benetti for their assistance in collecting fish. This study was supported by grants from the Italian Ministry of the University and from Scientific Research and Technology.

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