# Helminth communities in eels Anguilla anguilla from Adriatic coastal lagoons in Italy

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#### **Abstract**

The composition and diversity of the total and intestinal component and infra-communities were determined in eels Anguilla anguilla from three shallow lagoons on the Adriatic coast of Italy to determine whether the helminth communities would differ in composition and structure from those in eels from lagoons on the Tyrrhenian coast. The lagoons differed in respect of their management regimes and the extent of freshwater influx. Both freshwater and marine species of helminths were found in the eels in all three lagoons, but the freshwater component was richer in Valle Figheri. A suite of three digenean eel specialist species occurred in all three lagoons, of which any two members dominated each community. This conferred a high degree of similarity between the communities of the three lagoons. The same three species also dominated helminth communities in eels in lagoons along the Tyrrhenian coast of Italy, and compositional similarity levels were similar within and between western and eastern groups. Species richness was higher in the component communities of the eels of the Adriatic lagoons when compared to the Tyrrhenian ones, but diversity and dominance indices were of a similar order of magnitude and range. Intestinal helminth communities were richer and more diverse in two of the Adriatic lagoons because the proportion of eels with zero or one helminth species was, unusually, in the minority. It was nevertheless concluded that infracommunity structure was similar in eels from both western and eastern lagoons and that the hypothesis that it would differ in Adriatic lagoons could not be supported. The findings provide further evidence of the similarity in composition and structure of helminth communities in eels from coastal lagoons throughout Europe.

## Introduction

Most studies on helminth communities of the European eel *Anguilla anguilla* have been carried out in freshwater localities in the British Isles (Kennedy, 1990, 1993, 1997; Kennedy & Guégan, 1996). These indicate that

the communities are isolationist in character, being generally species poor and with a high dominance by one species, but are generally similar in structure if not composition (Kennedy, 1997). A major question now is how far the conclusions derived from this body of work can be applied to helminth communities in the European eel throughout the rest of its range on the Continent.

There is increasing evidence that conclusions derived from British studies can be applied to helminth

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component and infracommunities of eels from freshwater (Kennedy et al., 1998). Further support for this view comes from the studies of Schabuss et al. (1997), who also confirmed that the helminth component communities are isolationist and species poor, and of Sures et al. (1999), who showed that both component and infracommunities in eels of the River Rhine are similar in characteristics to those analysed from both the British Isles and the River Tiber. The situation with respect to eels from coastal lagoons is less clear. Even though such lagoons are common around the Mediterranean and Baltic seas, where they are often important sites of commercial fisheries and aquaculture, the helminth communities of their eels have seldom been studied. Those studies that do exist have often been qualitative in approach, and have focused on changes in helminth composition in relation to salinity (Seyda, 1973; Køie, 1988; Orecka-Grabda & Wierzbicka, 1994). The most detailed and quantitative analysis was carried out by Kennedy et al. (1997) on eels from four lagoons on the Tyrrhenian sea coast near Rome. Whilst freshwater helminths were present in some lagoons, the majority of species were of marine origin and communities were dominated by digeneans. Community composition was similar between lagoons, but differed from that in freshwater localities. Infracommunity structure, however, was similar in all four lagoons and also in communities from freshwater localities in Britain and the continental mainland, suggesting the operation of common structuring factors.

It is clearly desirable to extend such studies by investigating other coastal lagoons and the most obvious and appropriate basis for comparison is the lagoons from the Adriatic coast of Italy. The present paper, which forms part of an ongoing investigation into the parasites

of Italian eels (Kennedy et al., 1997, 1998), presents the results of an analysis of intestinal helminth community composition and structure in eels from three coastal lagoons from the Adriatic sea. Two are in the north, close to Venice and Ravenna respectively, and one in the south Adriatic. The fauna of the Adriatic sea is known to differ in many respects from that of the Tyrrhenian sea (Pérès, 1967) and so the investigation aimed to test the hypothesis that helminth community composition and structure in eels from the Adriatic would differ from those in eels from lagoons in western Italy (Kennedy et al., 1997).

#### Materials and methods

Three lagoons were selected for this study, as being representative of the fewer Italian east coast lagoons and with regard to the availability of eel samples from fishermen. Two were in the north of the Adriatic: the Valle Figheri, Venezia, and the Valli di Comacchio, Ferrara. The third lagoon is in the south of the Adriatic, the Lago di Acquatina, Lecce. Details of area and salinity are given in table 1. All three lagoons are shallow (mean depth 1 m or less) and connected to the Adriatic, although any exchange of water may be intermittent and seasonal and is never extensive. The two northern lagoons tend to suffer from increasing nutrient loading and so have dense phytoplankton. All three lagoons have some freshwater input. In Acquatina the eels are wild, but the other two lagoons support extensive eel farming. All three lagoons are used for aquaculture and the eels are commercially exploited: for further information on commercial stocks see Moriarty & Dekker (1997).

All cels were caught in fyke nets or traps by commercial fishermen. Samples were taken from each

Table 1. Selected characteristics of the helminth fauna of all eels from three Adriatic lagoons.

	Lagoons							
	Valle Figheri		Comacchio		Acquatina			
Lagoon area (km²)	Transfer of the	84.7		114.5		45		
Lagoon salinity range (%)		15-35		23–37		30-42		
No. of eels examined		33			42	21		
Mean length of eels (cm) (SD)		58.8 (3.3	3)	3.	5.3 (4.5)	51.1(9.3)		
Length range (cm)		53–66		26–46		39-71		
Parasites	Site	%	A	%	A	%	Λ	
Pseudodactylogyrus anguillae	G	54.5	10.3(21.4)	0	0	4.8	0.2(0)	
P. bini	G	3.0	0.1(0)	0	0	0	0	
Gyrodactylus anguillae	G	3.0	0.1(0)	0	0	0	0	
Bucephalus polymorphus	S/I	45.4	22.2(69.3)	2.4	0.1(0)	47.6	9.6(37)	
Deropristis inflata	I	93.9	38.6(60.9)	73.8	29.7(67)	19.0	0.3(0.9)	
Lecithochirium musculus	S	36.4	2.2(9.9)	69.0	2.3(6.6)	4.8	0.1(0)	
Helicometra fasciata	I	0	0	73.8	13.8(21.7)	0	0.1(0)	
Proteocephalus macrocephalus	I	9.1	0.3(2.5)	0	0	0	0	
Tetraphyllidea (larvae)	I	0	0	0	0	4.8	0.1(0)	
Contracaecum sp. (larvae)	BC	69.7	28.0(75.2)	9.5	0.2(1.5)	61.9	23.9(71.4)	
Anguillicola crassus	SB	9.1	0.4(6.3)	11.9	0.1(0.4)	0	0	
Cosmocephalus obvelatus (larvae)	BC	0	0	4.8	0.1(0)	0	0	
Acanthocephala (larvae)	I	12.1	0.21(1.4)	0	0	0	0	
Ergasilus gibbus	G	3.0	0.2(0)	0	0	0	0	

Key: %, prevalence; A, abundance (SD); G, gills; S, stomach; I, intestine; BC, body cavity; SB, swim bladder.

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Key: D.i., Deropri

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lagoon on one occasion only: from Valle Figheri on 26.03.99, from Valli di Comacchio on 22.12.97 and from Acquatina on 14.02.99. Sample sizes and dates were determined by the fishermen and were beyond the control of the authors. The mean lengths and ranges were comparable in Figheri and Acquatina, but were smaller in Comacchio (table 1).

Eels were brought back to the laboratory alive, frozen immediately and then examined at leisure. They were examined for helminth and crustacean parasites only by standard methods, from all organs except the blood system. Numbers of each parasite species in each eel were recorded and the total sample sizes are shown in table 1.

Analyses were undertaken at both component and infracommunity levels (sensu Holmes & Price, 1986). Measures of community structure and similarity adopted were those used in studies of helminth communities of eels from lagoons in the Tyrrhenian sea (Kennedy et al., 1997). The terms prevalence and abundance are used as defined by Bush et al. (1997). Measures of component community structure adopted were Species Richness, the Shannon-Weiner index and its evenness and the Berger-Parker Dominance index, whilst measures of infracommunity structure, carried out on intestinal species only, were the mean number of species and individuals per eel and the mean Brillouin's index. All indices were defined as in Magurran (1988) using natural logs (ln) where appropriate. Similarities were measured using Sorensen's index and the % similarity index at component community levels but only Sorenson's index was used at the infracommunity level. All analyses were carried out on the entire sample of eels, as individual samples were too small to be sub-divided by eel length.

Analyses at the component community level were carried out on the total community and the intestinal community separately. At the infracommunity level, all analyses were carried out on intestinal communities only. Data from other Italian lagoons that are included for comparison can be found in Kennedy *et al.* (1997).

# Results

### Community composition

Summary data on the composition of the helminth communities are presented in table 1. Freshwater species

(both Pseudodactylogyrus species, Gyrodactylus anguillae, Proteocephalus macrocephalus and Anguillicola crassus) were most common in Figheri but Pseudodactylogyrus anguillae was also found in Acquatina and A. crassus in Comacchio. The remaining species are all marine, and marine species were found in all three lagoons. The digeneans were the dominant group of helminths, and Deropristis inflata, an eel specialist, dominated both total and intestinal component communities in two of the three lagoons (table 2). In Acquatina, the nematode Contracaecum sp. dominated the total component community, and the digenean Bucephalus polymorphus the intestinal infracommunity. Species such as Ergasilus gibbus and larvae of Tetraphyllidea are not exclusively freshwater or marine, but are characteristic of lagoons with enhanced salinity levels. High prevalences of one or more of the three specialist digeneans D. inflata, B. polymorphus and Lecithochirium musculus are characteristic of all three lagoons. The composition of the helminth fauna reflects, amongst other factors, the salinity regime of the lagoon and Comacchio appears to be the most marine and Figheri the least. The only allogenic species present is Contracaecum sp., and its abundance probably reflects principally the extent of the bird definitive host use of each lagoon.

#### Community similarity

Similarity levels between the total component communities in the three lagoons and between these lagoons and those from the west of Italy are shown in table 3. Levels of total component similarity between the three lagoons on a qualitative basis (Sorensen's index) are high, between 0.55 and 0.61, and of a similar order of magnitude. These levels drop with the quantitative % similarity index, which still indicates the highest similarity as between Figheri and Acquatina, but with the highest value now 50%. This index also emphasizes the extent of the quantitative dissimilarity between Comacchio and Acquatina. In comparison with the helminth communities from the four lagoons in the west of Italy, those from the Adriatic exhibit a narrower range of Sorensen's index (0.55-0.61 compared to 0.33-1.0) but a slightly greater range of similarity as measured by the % similarity index (1.7–50.0 compared to 27.0–73.0). Comparisons between the helminth communities in the

Table 2. Diversity characteristics of the helminth communities of eels from Italian lagoons.

	Comacchio	Figheri	Acquatina	Range from Tyrrhenian lagoons
a. Total component community	ni e/Atmiledate			
No. of eels	42	33	21	20-44
No. of species	7	11	6	3–8
Shannon-Wiener Index	0.85	1.45	0.71	0.86-1.34
Shannon-Wiener evenness	0.44	0.60	0.40	0.63-0.97
Berger-Parker Index	0.64	0.38	0.70	0.34-0.67
Dominant species	D.i.	D.i.	Co.	B.p. and D.i.
b. Dominance of intestinal comp	onent community			
Berger-Parker Index	0.65	0.60	0.95	0.43-0.71
Dominant species	D.i.	D.i.	В.р.	D.i and B.p.

Key: D.i., Deropristis inflata; B.p., Bucephalus polymorphus; Co., Contracaecum.

Table 3. Indices of similarity between total helminth component communities of eels from Italian lagoons.

	Adriatic lagoons			Tyrrhenian lagoons				
	Comacchio	Figheri	Acquatina	Burano	Fogliano	Monaci	Caprolace	
Comacchio		0.55	0.59	0.40				
Figheri	40.0			0.40	0.73	0.73	0.60	
Acquatina		-	0.61	0.53	0.53	0.53	0.43	
	1.7	50.0	_	0.43	0.80	0.80	0.66	
Burano	42.0	57.0	12.0		0.33			
Fogliano	23.0	61.0	49.0	27.0	0.33	0.33	0.36	
Monaci	49.0	62.0		27.0	-	1.0	0.85	
Caprolace			30.0	52.0	66.0	_	0.85	
Capiolace	69.0	55.0	17.0	52.0	50.0	73.0	0.05	

Values above the diagonal are for Sorensen's index: values below the diagonal are for the % similarity index.

western and eastern lagoons indicate considerable similarity, with a range of 0.4–0.8 for Sorensen's index and 12–69% for the % similarity.

Levels of similarity between intestinal helminth component communities only exhibit a similar pattern (table 4a). Sorensen's index between the eastern lagoons shows a high but narrow range (0.66–0.75), whereas values for the % similarity index are in general lower and extend over a wider range (3.9–64.5). Yet again, the most dissimilar pair is Comacchio and Acquatina. These values compare favourably with those of the western lagoons: 0.4–1.0 for Sorensen's and 34–77% for the % similarity. Comparisons between the helminth communities in the western and eastern lagoons again indicate considerable similarity, within the range of 0.36–0.86 for Sorensen's index and 16–80% for the % similarity index.

Values of Sorensen's index only for intestinal infracommunities are shown in table 4b. Ranges are narrower in the eastern group (0.19–0.43) than within the western group (0.29–0.57). The range of similarities for western and eastern group together falls between 0.31 and 0.65. These values are generally lower than those for the component community comparisons, but it nevertheless appears that levels of similarity are of the same orders of magnitude between lagoons within each group and between groups. Much of the similarity is due to the presence of the suite of three digeanean species in most of the lagoons and to the domination of each by one of these three species. The most common dominant species is *D. inflata*, which dominated three of the four western lagoons and two out of three eastern ones (table 2). It is evident that there is no clear distinction between the helminth communities in the lagoons in the east and west of Italy.

# Component community structure

Diversity characteristics of the total component communities are summarized in table 2a. Figheri has the richest, most diverse and most even component community and Acquatina the poorest, least diverse and most uneven. In respect of richness and diversity, Comacchio and Aquatina are fairly similar even though they were the least similar in respect of component community composition. When comparing eastern and western lagoons, Figheri is similar in diversity characteristics to

Table 4. Indices of similarity between intestinal helminth component communities of eels from Italian lagoons.

		s	Tyrrhenian lagoons				
-13,414	Comacchio	Figheri	Acquatina	Burano	Fogliano	Monaci	Caprolace
a. All eels, comp	onent communities						1
Comacchio Figheri Acquatina Burano Fogliano Monaci Caprolace	64.5 3.9 53.4 26.1 48.6 69.9	0.66 - 38.8 66.9 59.8 82.3 80.2	0.66 0.75 - 16.4 47.0 45.8 19.6	0.36 0.60 0.40 - 34.4 56.9 66.4	0.75 0.86 0.86 0.44 - 77.5 53.9	0.75 0.86 0.86 0.44 1.0	0.75 0.86 0.86 0.44 1.0
o. Values are me Comacchio Pigheri Acquatina	eans of 25 randomly	selected pairs o 0.43 –	0.19	0.37	0.31 0.31	orensen's index 0.34 0.56	0.40 0.65
Burano Fogliano Monaci Caprolace				0.41	0.34 0.29	0.43 0.38 0.57	0.36 0.34 0.46 0.43

Values above the diagonal are for Sorensen's index: values below the diagonal are for the % similarity index.

Table 5. Div

No. of eels No. of help Mean SD No. of helm Mean SD Max No. of helm Mean SD Brillouin's Ir Mean SD Max Brillouin's In Mean SD

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Diversity nities of eel stand out, number of s considerably other lagoo causally, wit with 0 or 11 majority of uninfected. I is also highes is 3. By co infected eels Acquatina communities values for th comparable tions and he Figheri clearl unusually, th species. Neve in infected ea and especial

Table 5. Diversity characteristics of the intestinal helminth infracommunities of eels of Italian lagoons.

	Comacchio	Figheri	Acquatina	Range from Tyrrhenian lagoons
No. of eels	42	33	21	20-44
No. of helminths				
Mean	45.9	63.2	10.1	2.6-10.0
SD	59.9	76.6	27.8	3.9-18.8
No. of helminth spp.				
Mean	2.2	1.8	0.8	0.6-1.3
SD	0.8	0.9	0.8	0.7-0.8
Max	4	4	3	3–3
No. of helminth spp. (infected eels only	·)			
Mean	2.2	1.9	1.2	1.3-1.6
SD	0.8	0.9	0.6	0.6-0.6
Brillouin's Index				
Mean	0.37	0.22	0.03	0.07-0.17
SD	0.29	0.28	0.10	0.18-0.22
Max	1.08	1.07	0.46	0.56-0.75
Brillouin's Index (infected eels only)				
Mean	0.46	0.39	0.29	0.38-0.50
SD	0.26	0.26	0.25	0.10-0.29
Proportion of eels with 0 or 1 spp.	0.19	0.42	0.90	0.60 - 0.84

ame orders of h group and is due to the pecies in most ach by one of minant species four western (table 2). It is between the yeast and west

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mponent comigneri has the conent commuerse and most ty, Comacchio ogh they were nt community and western aracteristics to

> 0.75 0.86 0.86 0.44 1.0 1.0 -0.40 0.65 0.36 0.34 0.46

Burano and Fogliano, and Comacchio to Caprolace. Acquatina exhibits the lowest diversity of all the lagoons, but the value is still of a similar order of magnitude. This similarity is also evident in respect of the dominance of the intestinal component communities (table 2b). Five of the communities are dominated by the same species, *D. inflata*, and the other two by *B. polymorphus* and values of the Berger-Parker index are of similar orders of magnitude. There is thus no clear distinction in respect of diversity characteristics between the helminth component communities of eels in the east and west of Italy as diversity values and dominance levels are of similar magnitude within each group and between the two groups.

#### Infracommunity structure

Diversity characteristics of the intestinal infracommunities of eels are summarized in table 5. Two lagoons stand out, Commachio and Figheri, since the mean number of species, individuals and Brillouin's index are considerably higher than values for eels in any of the other lagoons. These values are associated, probably causally, with the much lower proportion of eels infected with 0 or 1 helminth species, as in all other lagoons the majority of eels harbour only one species or are uninfected. The maximum number of species per eel, 4, is also highest in these two lagoons: in all other lagoons it is 3. By contrast, the value of Brillouin's index for infected eels only is more similar across all lagoons. Acquatina undoubtedly harbours the least diverse communities, though not the least species rich, and values for the indices for Acquatina are generally more comparable to those from the western lagoons. Conditions and helminth population levels in Comacchio and Figheri clearly favour high rates of transmission and so, unusually, the majority of eels harbour two or more species. Nevertheless, the diversity of infracommunities in infected eels as judged by the mean Brillouin's index and especially the mean Brillouin's index for infected

eels only is very similar to that recorded from the western lagoons.

#### Discussion

The helminth communities of eels in the Adriatic lagoons comprise both freshwater and marine species. The marine species predominate in each lagoon, and the prevalance and abundance of the freshwater species must relate to the individual conditions in the lagoon and especially to the water management regime and the extent of the freshwater input. The greatest number of freshwater species were found in Valle Figheri, but a freshwater species was present in each of the other two lagoons. Other individual differences such as the high prevalence and abundance of Contracaecum sp. in two lagoons and the low levels in Comacchio must relate to the use of the lagoons by the bird definitive hosts. What impresses more than the differences is the similarity in composition. Intestinal helminth communities in all three lagoons are dominated by two out of three species of specialist marine digeneans. A similar domination by marine digeneans was reported from the lagoons in western Italy (Kennedy et al., 1997) and from the American eel A. rostrata in estuarine conditions (Crane & Eversole, 1989). In freshwater, communities are dominated by acanthocephalans in Europe (Kennedy, 1990) and domination by digeneans is known only from Australia (Kennedy, 1995). The composition of the helminth communities is very similar in both the western and eastern Italian lagoons. Altogether 14 species were reported from the Adriatic lagoons and ten from the Tyrrhenian ones, of which seven were common to both groups. Included in this common suite are the three dominant species of digeneans. Some species were found only in the Adriatic lagoons, including Helicometra fasciata and Cosmocephalus obvelatus, and some, such as Goezia anguilla, only in the western lagoons. Some of these localized species, such as G. anguilla and Ergasilus

gibbus, are known to have wide distributions, and their presence in only one lagoon in each case may reflect chance, or the single, small sample. Marine digeneans appear also to be common in eels in the Baltic sea (Køie, 1988) and to a lesser extent in Polish estuarine waters (Orecka-Grabda & Wierzbicka, 1994). Lagoons appear to be the preferred habitat of *D. inflata, L. musculus* and *B. polymorphus*. The communities in each group of lagoons do differ in composition between individual lagoons within a group and between groups, but not as much as

might be expected.

It is this same suite of digeneans, together with the frequent dominance of D. inflata, that are responsible for the high levels of similarity within and between each lagoon group. This species is always present, generally common and often abundant. Of the other two species in this suite, B. polymorphus also occurred in all the lagoons, but was less abundant except in Valle Figheri. Lecithochirium musculus was present in all the lagoons except Burano, but it was never very abundant. The species that were very local in distribution, such as P. macrocephalus, Telosentis exiguus and E. gibbus, generally occurred at low abundance levels and so had little influence on the quantitative % similarity index. The notable exception to this generalization was H. fasciata in Comacchio as this was found only in this lagoon and then at high prevalence and abundance. This may be the reason for similarities with Comacchio often being rather lower. Communities in Acquatina also exhibited some peculiarities that would have been responsible for its distinctiveness and the lower levels of similarity between this lagoon and others, and especially Comacchio: the community was species poor, abundances of D. inflata and L. musculus were low and neither component nor infracommunities were dominated by D. inflata. The pattern that emerges from a consideration of similarities is that there is no clear distinction between the eel parasite communities of lagoons of the Adriatic sea and the Tyrrhenian sea. Communities are as similar and dissimilar within each group as they are between the groups of lagoons, and this is the case whichever index is used and for total component communities, intestinal component communities and intestinal infracommunities. Eels in coastal lagoons have a characteristic and broadly similar helminth community regardless of the location of the lagoon.

A consideration of the richness and diversity characteristics of the helminth communities leads to a similar conclusion. Amongst the Adriatic lagoons, helminth component communities in eels were richest and most diverse in Valle Figheri but values of diversity and dominance were of a similar order of magnitude to those in Fogliano in the west of Italy. Diversity and dominance values for the communities in the other two eastern lagoons were of a similar order of magnitude to those from Caprolace in the west. In five of the seven lagoons, intestinal component communities were dominated by the same species, D. inflata, and dominance index values were of a similar order of magnitude in eastern and western lagoons. There is no clear division of the helminth component communities between east and west in respect of diversity, dominance and richness at the component community level.

The situation is not quite as clear at infracommunity level, since intestinal helminth communities were richer, more diverse and more abundant in Comacchio and Figheri. This appears to be causally related to the unusually low proportion of eels in these two lagoons harbouring 0 or 1 species of helminth: these are a minority whereas in all other lagoons these are a majority. By contrast, the infracommunities in Acquatina are indistinguishable in their characteristics from those in the western lagoons. If the proportion of eels with 0 or 1helminth species, i.e. with zero diversity is ignored, and the focus is directed to species richness and diversity in infected eels only, the distinction between infracommunities in Comacchio and Figheri and the other lagoons tends to disappear. Mean species richness in these two lagoons is still higher than in all the others, but diversity is not and the values for Brillouin's index of 0.388 and 0.456 fall within the range of the western lagoons of 0.383-0.499. The maximum number of species per eel is higher in the two lagoons, but does not exceed 4: the maximum value found also in infracommunities in freshwaters in Europe (Kennedy, 1993, 1997; Kennedy & Guégan, 1996; Kennedy et al., 1998). The individuality of communities from Acquatina amongst the Adriatic group of lagoons may be a reflection of its smaller size and/or its isolation from the other lagoons (Poulin & Morand, 1999).

Overall, the findings provide no support for the hypothesis that helminth parasite communities in eels will differ between lagoons on the Tyrrhenian coast and on the Adriatic coast of Italy. The communities are more similar in composition and structure, despite some individuality in lagoons, than would be expected on this hypothesis and they cannot be separated into two clear groups. The hypothesis must therefore be rejected. It appears that the composition of helminth communities in eels in lagoons is broadly similar not just throughout Italy but also throughout Europe, as a comparison between the data presented here with those from lagoons in western Italy (Kennedy et al., 1998) and the Baltic (Seyda, 1973; Køie, 1988; Orecka-Grabda & Wierzbiska, 1994) will indicate. Eels in saline lagoons harbour helminth parasite communities that are similar in composition and structure wherever they are, and indeed the structure of these communities is similar in eels from lagoons and freshwater habitats (Kennedy, 1993, 1997: Kennedy & Guégan, 1996; Kennedy et.al., 1997, 1998). The present findings thus provide further support for the suggestion made in the above publications that there are common, stabilizing, determinant factors operating to produce this underlying similarity.

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