Salinity dependence of parasite infestation in the European eel *Anguilla anguilla* in northern Germany

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The aim of the study was to examine metazoan parasite communities of European eels (*Anguilla anguilla*) in fresh-water, brackish water and marine localities in northern Germany. In all, 29 parasite species/taxa were found in 170 eels: eight digeneans, one monogenean, five cestodes, ten nematodes, two acanthocephalans, and three crustaceans. Measures of diversity characteristics of the helminth communities included species richness, Shannon's diversity index and its evenness, and the Berger–Parker dominance index. The highest species diversity and lowest dominance values were calculated for the helminth communities of eels from the two Baltic Sea localities. Parasite communities of European eels clearly exhibit the habitat preferences of their hosts, salinity-dependent specificities, and a clustering into fresh-water, brackish, and marine groups. The highly pathogenic parasite species *Anguillicola crassus* and *Pseudodactylogyrus* spp. were found at all sampling sites in fresh water and brackish water, with high prevalence. Basic information is provided on the risks of restocking programmes solely focusing on fresh-water sites.

Keywords: *Anguilla anguilla*, *Anguillicola crassus*, diversity, Germany, parasite communities, *Pseudodactylogyrus* spp., salinity, silver index.

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Introduction

After some three decades of decreasing catches and a dramatically reduced recruitment of glass eels to the European coast, the European Commission released a regulation (EC, 2007) with the objective of protection and sustainable use of the stock of European eels (*Anguilla anguilla*). All member states are obliged to develop eel management plans for their river basin districts, designed to reduce anthropogenic mortalities. One of the measures proposed to implement such a management plan successfully is restocking of juvenile eels to suitable habitats. However, the suitability of waterbodies for the production of healthy spawners is not only influenced by fishing pressure and connectivity to the open ocean, but also by the occurrence of diseases and parasites.

Most studies on the parasite fauna of the European eel have been carried out in fresh-water environments (e.g. Conneely and McCarthy, 1986; Køie, 1988a; Kennedy, 1993, 1997; Schabuss *et al.*, 1997; Kennedy *et al.*, 1998; Sures *et al.*, 1999; Di Cave *et al.*, 2001; Aguilar *et al.*, 2005; Kristmundsson and Helgason, 2007). Investigations on the parasite fauna of European eels in marine habitats (Outeiral *et al.*, 2001, 2002; Kristmundsson and Helgason, 2007) are scarce. Only a few comparable studies actually focused on changes in the parasite composition of eels in relation to salinity (Seyda, 1973; Køie, 1988b; Orecka-Grabda and Wierzbicka, 1994). The most detailed and quantitative analyses, including diversity indices, were carried out by Kennedy *et al.* (1997) on eels from four lagoons along the Tyrrhenian coast near Rome, and by Di Cave *et al.* (2001) on eels from Italian Adriatic coastal lagoons. Those studies showed that the helminth communities of Mediterranean eels are similar in composition and community structure to fresh-water habitats, although they differ in their generally reduced species diversity and the dominance of single parasite taxa. Therefore, those authors hypothesized a general trend of declining species richness and diversity with increasing salinity for European eels (Kennedy *et al.*, 1997). Comparable data for the closely related American eel (*Anguilla rostrata*) are largely missing, because the few similar investigations dealt more with the effects of geographic distance (Barker *et al.*, 1996) on parasite species richness and diversity, irrespective of the influence of salinity.

Here, we carried out a comparative examination for the first time on metazoan parasite communities of eels from fresh-water, brackish water, and marine localities of northern Germany, focusing on the swimbladder nematode *Anguillicola crassus* and the gill monogenean *Pseudodactylogyrus* spp. These eel parasites were introduced into western European water bodies as a result of uncontrolled intercontinental transfer of live eels for consumption (Køie, 1991), and they are considered serious pathogens (Kennedy, 2007). Infection with *A. crassus* reduces the functionality of the swimbladder as a hydrostatic organ and is feared to influence the ability of eels to migrate to their spawning grounds in the Sargasso Sea (Kennedy, 2007). *Pseudodactylogyrus* spp. appear to cause less pronounced effects in wild eels, but they can cause economically important losses in eel farms (Kennedy, 2007).

After an investigation of the Sr/Ca ratio in the otoliths of eels from fresh water and the sea, Tsukamoto *et al.* (1998) concluded

that eels should be regarded as facultatively catadromous, with ocean residents considered to be a distinct ecophenotype. Those authors further hypothesized that only eels that grow in the sea contribute to eel recruitment, because none of the 19 maturing silver eels caught in the ocean in their investigation were derived from fresh-water migrants. By investigating the salinity dependence of parasite infestation in the European eel, we aimed to test the ecophenotype hypothesis of Tsukamoto *et al.* (1998) and to provide basic information on the risks of restocking programmes solely focusing on fresh-water sites.

Material and methods

Sample collection and measurements

In all, 170 eels from six different sample sites in northern Germany (Figure 1) were taken from commercial fishers' fykenets between April and October 2006, including two fresh-water localities (Lake Plön and River Eider), three brackish localities of the western Baltic Sea (near Maasholm, the Kiel Bay near Friedrichsort, and the Fehmarn Belt), and one marine locality (the Helgoland coast). The salinity of the brackish water localities ranged between 15 and 26, and of the marine locality between 32 and 35. Eels were transported on ice to the laboratory and kept frozen at -40°C until examination.

For each eel, body mass (M), total length (L_T), pectoral fin length (L_{PF}), and vertical and horizontal diameters of both eyes were measured, and the mean eye diameter (E_D) was calculated (Table 1). Eels were dissected and gonad mass (M_G), liver mass (M_L), and gut mass empty weight (M_{GU}) were determined (Table 1). The gonadosomatic index ($I_G = 100\, M_G\, M^{-1}$), hepatosomatic index ($I_L = 100\, M_L\, M^{-1}$), gut index ($I_{GU} = 100\, M_{GU}\, M^{-1}$), and Fulton's condition factor ($K = 10^5\, ML_T^{-3}$) were calculated (Table 1). A "silver index" (Durif and Elie, in press), based on the external body measurements L_T, M, L_{PF}, and E_D, was applied to classify eels into six groups of maturation. These groups represented growth phases of undifferentiated stage I and female stage II (FII) eels, a pre-migrant stage (FIII), and migrant stages (FIV, FV, MII) for male (M) and female (F) eels.

Parasitological examination

Eyes, skin, fins, gills, nostrils, and the mouth cavity of each eel were examined for ectoparasites. Eyes and gills were removed and placed in separate Petri dishes with physiological saline, then examined under a stereomicroscope. To study the internal organs for endoparasites, each eel was dissected and its body cavity and mesenteries examined for encysted or encapsulated parasites. All internal organs were placed in separate Petri dishes in physiological saline, then examined. The swimbladder was examined macroscopically for the presence of pre-adult and adult *A. crassus* in the lumen, and for pathological alterations of the tissue. Larvae were counted by pressing the swimbladder between the lid and the base of a Petri dish under the stereomicroscope. Heart, liver, and spleen were examined by pressing the tissue between the lid and the base of a Petri dish under the stereomicroscope. Stomach and intestinal contents were mixed with saline and examined separately under a stereomicroscope. All isolated parasites were fixed and preserved in 70% ethanol. Acanthocephala were transferred to distilled water to induce an eversion of the proboscis before fixation. For identification, Digenea, Nematoda, and Acanthocephala were transferred into 100% glycerine (Riemann, 1988). Cestoda were stained in acetic carmine, dehydrated in a gradated ethanol series, cleared with methyl-salicylate, and mounted in Canada balsam.

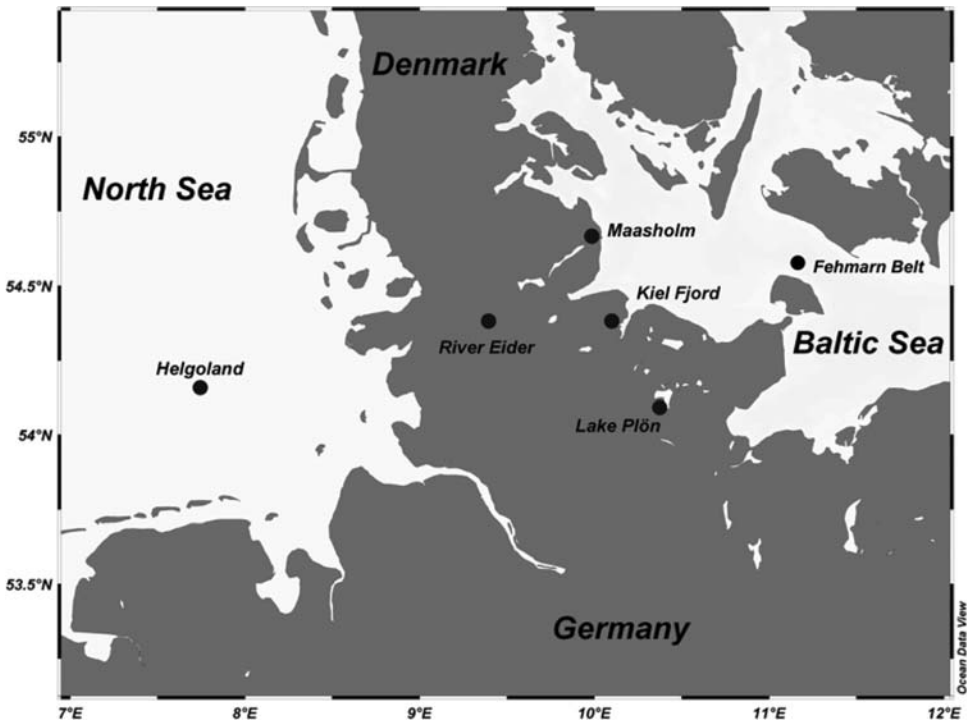

Figure 1. Sampling sites for eels in northern Germany from the fresh-water Lake Plön and River Eider, the brackish Friedrichsort (Kiel Fjord), Maasholm, and Fehmarn Belt, and the marine locality Helgoland (map source, Ocean Data View; Schlitzer, 2007).

Table 1. Mean values (±s.d.) of total length (L_T), body mass (M), pectoral fin length (L_{PF}), mean eye diameter (E_D), Fulton's condition factor (K), gonadosomatic index (I_G), gut index (I_{GU}), and hepatosomatic index (I_L) for eels from two fresh-water (F), three brackish (B), and one marine (M) locality.

Parameter	Lake Plön (F)	River Eider (F)	Friedrichsort (B)	Maasholm (B)	Fehmarn Belt (B)	Helgoland (M)
L_T (cm)	91.7 ± 6.7	49.7 ± 11.9	63.9 ± 9.6	71.5 ± 7.4	84.6 ± 5.0	59.4 ± 8.5
M (g)	1 641.4 ± 357.9	301.2 ± 297.9	486.2 ± 357.9	748.2 ± 174.1	1 327.4 ± 221.7	356 ± 174.1
E_D	10.24 ± 1.01	5.43 ± 1.37	6.28 ± 1.03	6.52 ± 0.55	9.03 ± 0.63	5.97 ± 0.96
L_{PF}	42.86 ± 3.67	20.23 ± 6.56	24.53 ± 3.95	28.24 ± 3.73	37.11 ± 3.47	22.19 ± 3.57
K	0.21 ± 0.03	0.2 ± 0.03	0.17 ± 0.02	0.19 ± 0.03	0.22 ± 0.02	0.16 ± 0.02
I_G	1.27 ± 0.24	0.18 ± 0.24	0.68 ± 0.47	0.73 ± 0.28	1.38 ± 0.22	0.57 ± 0.27
I_{GU}	1.26 ± 0.27	3.34 ± 0.43	1.92 ± 0.49	1.97 ± 0.68	0.82 ± 0.31	2.46 ± 0.51
I_L	1.29 ± 0.15	1.69 ± 0.39	1.23 ± 0.33	1.35 ± 0.35	1.10 ± 0.16	1.22 ± 0.26

The parasitological terminology used follows Bush *et al.* (1997): prevalence (P) is the number of hosts infected with one or more individuals of a particular parasite species divided by the number of hosts examined (expressed as a percentage); intensity (of infection, I) is the number of individuals of a particular parasite species in a single infected host (expressed as a numerical range), and mean intensity (mI) is the mean number of individuals of a particular parasite species per infected host in the sample.

Analyses of parasite community structure were carried out at a component level (Holmes and Price, 1986). Measures used to describe component community structure of the helminth parasites (including Monogenea) were species richness (s), Shannon's diversity index (H') and evenness (E), and the Berger–Parker dominance index (d). Formulae for each of these variables were (Magurran, 1988):

$$H' = -\sum p_i \ln p_i,$$

where p_i is the proportion of individuals of each species in the sample to the total number of individuals in the sample (n_i/N);

$$E = \frac{H'}{H_{\max}},$$

where $H_{\max} = \ln s$, s being the total number of species in the sample (the species richness);

$$d = \frac{N_{\max}}{N},$$

where $N_{\max}$ is the number of individuals of the most abundant species, and N the total number of individuals at each site.

Statistics

A median test (Kruskal–Wallis ANOVA) was used to compare the values of median intensity of infection with *A. crassus* and *Pseudodactylogyrus* spp. of eels among the different localities. To test the effect of *A. crassus* and *Pseudodactylogyrus* spp. infection on the condition indices I_G, I_L, I_{GU}, and K of the eels, a correlation analysis was performed. In all tests, we defined statistical significance as being at the 5% level. Statistics were performed using STATISTICA Version 6. To visualize similarities in parasite communities of eels at the various localities, a hierarchical cluster analysis (complete linkage) was performed using Primer Version 6.1.6. The data for this analysis used arcsine-transformed prevalence of infection values.

Results

Parasite community composition and structure

In all, 29 metazoan parasite species/taxa (eight digeneans, one monogenean, five cestodes, ten nematodes, two acanthocephalans, three crustaceans) were observed in 170 eels from the six northern German habitats investigated (Table 2). The most prevalent parasite taxa in fresh water were cestodes and nematodes, but in the sea, eels were infested mainly with digeneans.

Parasite species richness (s), including Crustacea, was highest in eels caught from the Fehmarn Belt (brackish) and from Lake Plön (fresh water), with 16 and 13 species/taxa, respectively (Table 2). Eels from the River Eider and from the brackish waters near Maasholm harboured 11 species/taxa each, followed by Kiel Bay near Friedrichsort (brackish) with 9 species/taxa, and the marine site near Helgoland with 7 species/taxa (Table 2). The diversity characteristics of the helminth component community structure revealed high parasite species diversity and low dominance values in eels from the three brackish localities (Table 3). The most diverse community was detected in the eels from Maasholm ($H' = 1.83$), with highest evenness ($E = 0.76$) and lowest dominance ($d = 0.27$) values. The diversity indices of the helminth parasite community of Helgoland ($H' = 0.56$) and River Eider eels ($H' = 0.55$) were the lowest, whereas their dominance values were highest. Both communities were dominated by a single parasite species: Helgoland eels by the digenean *Lecithochirium rufoviride*, and River Eider eels by the monogenean *Pseudodactylogyrus* spp., verified by high Berger–Parker dominance values of 0.80 and 0.88, respectively. Only two localities, the fresh-water site at the River Eider and the brackish site near Friedrichsort, were dominated by the monogenean genus *Pseudodactylogyrus*, and the other localities by digeneans (Table 3). Cluster analysis of parasite prevalence data reveals a clear habitat specific composition and a clustering into fresh-water (Lake Plön and River Eider), brackish (Friedrichsort, Maasholm, and Fehmarn Belt), and marine (Helgoland) groups (Figure 2).

Anguillicola crassus and *Pseudodactylogyrus* spp.

Anguillicola crassus was more prevalent in fresh water (P = 83.3–93.3%) than in brackish (P = 40–46%) or marine (P = 0%) water (Figure 3a). There was no significant difference in the mean intensity of infection with *A. crassus* ($p = 0.06$) between eels caught at the different localities (Figure 3b). *Pseudodactylogyrus* spp. showed

Table 2. Composition of parasite communities with information on prevalence (P, percentage of eels infected), mean intensity (mI, mean number of parasite individuals per infected host), and intensity (I, number of parasites per infected host) of infection in eels from the fresh-water (F) localities Lake Plön and River Eider, the brackish (B) localities Friedrichsort, Maasholm, and Fehmarn Belt, and the marine (M) locality Helgoland.

Locality			**Lake Plön (F)**			**River Eider (F)**			**Friedrichsort (B)**			**Maasholm (B)**			**Fehmarn Belt (B)**			**Helgoland (M)**		
Length range (in cm)			**81–106**			**37–82**			**45–81**			**58–96**			**73–95**			**40–73**		
Sample size			**30**			**30**			**30**			**30**			**30**			**20**		
Number of parasite species, *s*			**13**			**11**			**9**			**11**			**16**			**7**		
Taxon	**Stage**	**Status**	**P**	**mI**	**I**	**P**	**mI**	**I**	**P**	**mI**	**I**	**P**	**mI**	**I**	**P**	**mI**	**I**	**P**	**mI**	**I**
Digenea																				
Diplostomum spathaceum	L	G	100	5.2	1–15	10	1.3	1–2	–	–	–	3.3	4	4	20	3.5	1–8	–	–	–
Lecithochirium rufoviride	A	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	90	45.8	7–193
Helicometra fasciata	A	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	80	12.5	1–37
Podocotyle atomon	A	G	–	–	–	–	–	–	33.3	4.3	1–11	43	10.8	1–56	20	4.3	2–8	5	1	1
Depropristis inflata	A	S	–	–	–	–	–	–	40	10.8	1–64	46	9.7	1–56	36.6	34.6	1–180	20	1.3	1–2
Brachyphallus crenatus	A	G	–	–	–	–	–	–	–	–	–	–	–	–	6.66	12.5	11–14	–	–	–
Plagioporus sp.	A	–	63.3	109.7	1–1 630	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Digenea indet.	A	–	–	–	–	–	–	–	–	–	–	3.3	1	1	–	–	–	5	1	1
Monogenea																				
Pseudodactylogyrus spp.	A	S	86.6	11	1–95	100	64.3	3–236	43.3	26.2	1–202	46	4.8	1–36	76	11.26	1–62	–	–	–
Cestoda																				
Proteocephalus macrocephalus	A	S	86.6	5.7	1–19	50	3.1	1–8	16.6	5.2	1–18	13.3	2.8	1–5	3.3	5.8	1–12	–	–	–
Bothriocephalus claviceps	A	S	60	2.3	1–5	46	3	1–9	–	–	–	–	–	–	13	1	1	–	–	–
Tetraphyllidea indet. (*Scolex pleuronectis*)	L	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	1	1
Proteocephalus sp.	A	–	43.3	6.6	1–19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cestoda indet.		–	13.3	1.3	1–2	3.3	1	1	3.3	1	1	–	–	–	3.3	1	1	–	–	–
Nematoda																				
Eustrongylides mergorum	L	G	53.3	2.1	1–4	–	–	–	–	–	–	–	–	–	10	4.3	1–8	–	–	–
Contracaecum sp.	L	–	20	2.2	1–4	–	–	–	13.3	1	1	23	6.1	1–26	33.3	5.4	1–2	–	–	–
Hysterothylacium aduncum	A	G	–	–	–	–	–	–	–	–	–	–	–	–	3.3	4	4	10	1	1
Camallanus lacustris	A	G	83.3	22.2	1–79	13.3	7.5	1–21	3.3	1	1	–	–	–	10	1.3	1–2	–	–	–
Anguillicola crassus	A	S	93.3	4.7	1–12	83.3	3.76	1–13	40	3	1–14	46	4.5	1–24	40	2.4	1–10	–	–	–
Pseudocapillaria tomentosa	A	G	10	1.3	1–2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anisakis simplex	L	G	–	–	–	–	–	–	–	–	–	3.3	3	3	–	–	–	–	–	–
Raphidascaris cf. *acus*	PA	G	–	–	–	3.3	2	2	–	–	–	–	–	–	–	–	–	–	–	–

Continued

Table 2. *Continued*

Taxon	Stage	Status	P			ml			l			P			P			P		
Paraquimperia tenerrima	A	S	–	–	–	–	–	–	–	–	–	23	6	1–22	–	–	–	–	–	–
Paraquaria adunca	L	G	–	–	–	–	–	–	–	–	–	–	–	–	3.3	9	9	–	–	–
Acanthocephala																				
Paratenuisentis ambiguus	A	–	–	–	–	20	5.3	1–26	–	–	–	–	–	–	–	–	–	–	–	–
Paratenuisentis cf. *ambiguus*	A	–	–	–	–	–	–	–	–	–	–	6.6	1	1	–	–	–	–	–	–
Acanthocephala indet.	A	–	–	–	–	–	–	–	–	–	–	–	–	–	3.3	1	1	–	–	–
Crustacea																				
Ergasilus gibbus	A	S	3.3	1	1	30	2.3	1–5	–	–	–	–	–	–	3.3	1	1	–	–	–
Lernaeocera branchialis	A	G	–	–	–	–	–	–	13.3	1.8	1–3	–	–	–	–	–	–	–	–	–
Argulus foliaceus	A	G	–	–	–	3.3	1	1	–	–	–	–	–	–	–	–	–	–	–	–

Stage of parasite maturity (L, larva; A, adult; PA, pre-adult) and status in the host (S, specialist; G, generalist) are given for each species of parasite.

Table 3. Component community structure of helminth parasites and their diversity characteristics in eels from the fresh-water (F) Lake Plön and River Eider, the brackish (B) water Friedrichsort, Maasholm, and Fehmarn Belt, and the marine (M) locality Helgoland.

Locality	Lake Plön (F)	River Eider (F)	Friedrichsort (B)	Maasholm (B)	Fehmarn Belt (B)	Helgoland (M)
Number of eels examined	30	30	30	30	30	20
Number of helminth species, *s*	12	9	8	11	15	7
Shannon's diversity index, H'	1.42	0.55	1.21	1.83	1.67	0.56
Shannon's evenness, *E*	0.57	0.25	0.58	0.76	0.62	0.29
Berger–Parker dominance index, *d*	0.59	0.88	0.59	0.27	0.47	0.80
Dominant species	P.sp.	P.spp.	P.spp.	P.a.	D.i.	L.r.

P.sp., *Plagioporus* sp.; P.spp., *Pseudodactylogyrus* spp.; P.a., *Podocotyle atomon*; D.i., *Deropristis inflata*; L.r., *Lecithochirium rufoviride*.

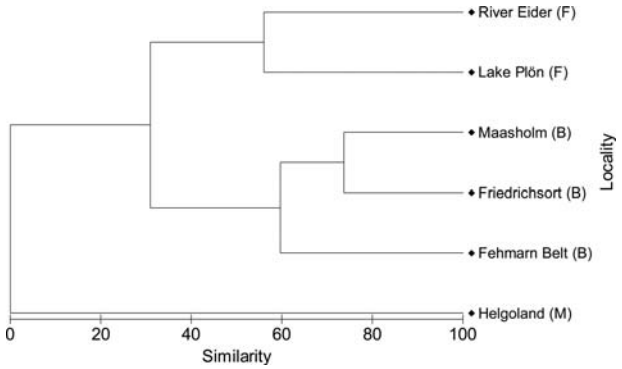

Figure 2. Hierarchical cluster analysis of similarity between all localities studied based on their parasite communities. B, brackish; F, fresh water; M, marine.

the same trend and was isolated with high prevalence in fresh water (P = 86.6–100%), moderate to high in brackish water (P = 43.3–76%), and was not detected in the sea (Figure 3c). A significantly higher intensity of infection with *Pseudodactylogyrus* spp. was detected for the River Eider eels ($p < 0.05$; Figure 3d). The Berger–Parker dominance index revealed *Pseudodactylogyrus* spp. as the dominant species in eels from the River Eider ($d = 0.88$) and Friedrichsort ($d = 0.59$; Table 3). A correlation analysis of infection with *A. crassus* as well as with *Pseudodactylogyrus* spp. related to I_G, I_L, I_{GU}, and K revealed no relationship ($p < 0.05$).

Eel maturation stage

Maturation stage determination revealed 15 undifferentiated stage I eels, 65 female stage II eels (growth phase), 29 pre-migrating female stage III eels (pre-silver stage), 60 migrating female stage

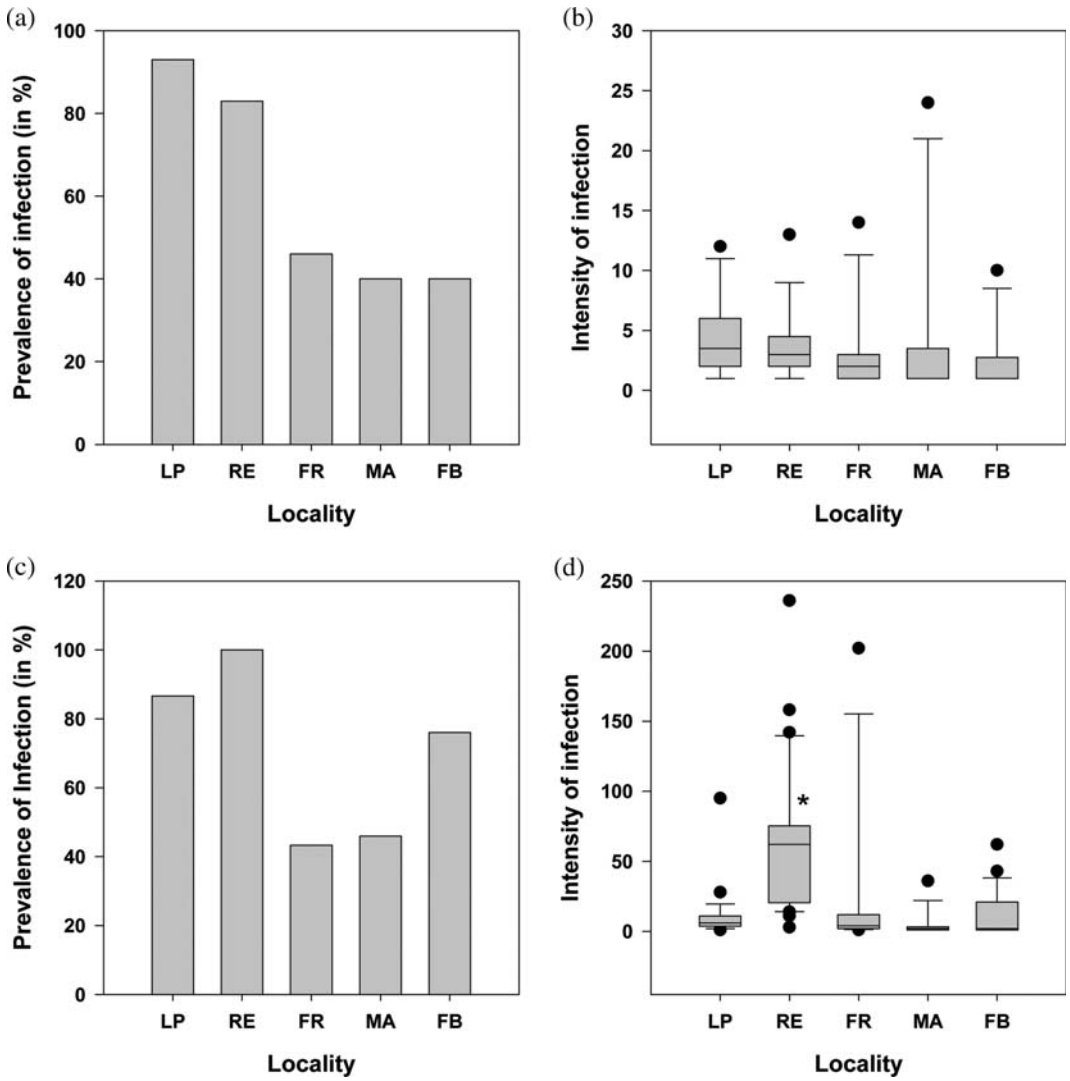

Figure 3. Prevalence and intensity of infection for (a and b) *A. crassus*, and (c and d) *Pseudodactylogyrus* spp. for the fresh-water Lake Plön (LP) and River Eider (RE), and the brackish water Friedrichsort (FR), Maasholm (MA), and Fehmarn Belt (FB). Box plots show the median values for intensity of infection (line within the box), the boundaries of the boxes indicate the 25th and 75th percentiles, the whiskers above and below the box the 90th and 10th percentiles, and the large dots the outlying points. The asterisk indicates a significant difference in intensity of infection ($p > 0.05$, median test).

Table 4. Mean total length ($L_T \pm$ s.d.) and percentage of eels in each of five stages of maturation for eels collected from two fresh-water (F), three brackish water (B), and one marine (M) locality.

Locality	*n*	Mean L_T (cm) $\pm$ s.d.	Maturation stage (%)				
			Growth phase		Pre-migrant	Migrant	
			I	FII	FIII	FIV	FV
Lake Plön (F)	30	91.7 $\pm$ 6.7	0	0	6.6	93.3	0
River Eider (F)	30	49.7 $\pm$ 11.9	40	46.6	6.6	6.6	0
Friedrichsort (B)	30	63.9 $\pm$ 9.6	3.3	73	20	0	3.3
Maasholm (B)	30	71.5 $\pm$ 7.4	0	50	40	10	0
Fehmarn Belt (B)	30	84.6 $\pm$ 5.0	0	0	10	90	0
Helgoland (M)	20	59.4 $\pm$ 8.5	10	70	20	0	0

Undifferentiated stage I and female stage II (FII), growth phase; female stage III (FIII), pre-migrant stage; female stages IV and V (FIV and FV), migrant stages.

IV eels, 1 migrating female stage V eel, but no male eels. The distributions of the maturation stages at each locality differ (Table 4). Eels from Lake Plön and Fehmarn Belt were the most developed, with mean L_T values of 91.7 and 84.6 cm, respectively (Table 4). The samples consisted of ~90% female stage IV eels. The River Eider eels were the most undifferentiated and the smallest, with 40% stage I and a mean L_T of 49.7 cm (Table 4).

Discussion

Size- and age-dependence of parasite infestation

The intensity of infection of metazoan parasites in fish populations increases with age or size of the host, because parasite accumulation is a time-driven process (Dogiel *et al.*, 1958). The high species richness and diversity of the Fehmarn Belt eels ($s = 15$, $H' = 1.67$) can therefore be explained largely by their considerably larger size (mean $L_T = 84.6$ cm) and later developmental stage (90% stage IV). These migrating silver eels were most probably an assemblage of eels of different origin, because the Fehmarn Belt forms a bottleneck for eels migrating from east of Fehmarn to the North Sea and on to the Sargasso Sea. Possible origins east of Fehmarn include the Baltic Sea proper and the adjacent river systems. Different migration paths are also supported by the high species richness and component community structure. Low species richness and diversity of the parasite fauna of the River Eider ($s = 9$, $H' = 0.55$) most likely reflect the overall smaller body length (mean $L_T = 49.7$ cm) and therefore earlier maturation stages (40% stage I, 46.6% stage II) of their hosts.

Dominance

Direct competition of parasites within a host can result in strong dominance (Poulin, 1999), reflected by low Shannon's diversity and higher Berger–Parker dominance indices. Values for the Berger–Parker dominance index were relatively high for all localities except for the western Baltic Sea site near Maasholm. The highest values were calculated for Helgoland and the River Eider. These results support the hypothesis of Kennedy *et al.* (1997) that parasite communities of the European eel are characterized by low species diversity and high dominance of a single parasite species, although the dominant species can vary. From our study, though, we did not confirm the general dominance of acanthocephalans as eel parasite communities in fresh water, suggested by Kennedy *et al.* (1998). The greatest prevalence (20%) of an acanthocephalan, *Paratenuisentis ambiguus*, was detected in eels from the River Eider, whereas the prevalence of infection of the Maasholm (6.6%; *Paratenuisentis* cf. *ambiguus*) and Fehmarn Belt samples (3.3%; Acanthocephala indet.) was rather low.

Salinity-dependence of parasite community structure

Parasite communities of the European eel clearly reflect the habitat preferences of their hosts. Despite overall similarities in parasite species composition, salinity-dependent specificities are well supported and reflect the life history of individual eels. The strictly host-specific, introduced parasites *A. crassus* and *Pseudodactylogyrus* spp. could not be found in the marine environment of the North Sea. Their restriction to fresh and brackish waters, where they occur with high prevalence, might affect the locality-specific survival of eels, and therefore contribute to recruitment success. However, salinity-dependence is also evident for autochthonous parasite species such as the cestode *Proteocephalus macrocephalus* and the digeneans *Podocotyle atomon* and *Deropristis infalta*, which can be regarded as purely fresh-water- and seawater-specific, respectively. Although parasite species richness and diversity are considerably reduced in the marine environment of the North Sea around Helgoland, we cannot confirm the hypothesis of Kennedy *et al.* (1997) that these declines follow a clear salinity gradient. On the contrary, the intermediate salinity conditions of the brackish Baltic Sea seem to favour parasites in eels by integrating both marine and fresh-water species.

Implications for the management of eels

Owing to the relatively low intensities of infestation with autochthonous parasites, a negative effect on the health of their eel hosts that would impair their reproductive success can be excluded. Nonetheless, the recently introduced and highly pathogenic parasites *A. crassus* and *Pseudodactylogyrus* spp. were found at all investigated fresh- and brackish water sampling sites at high prevalence. Although infestation intensities and observed pathological alterations of the swimbladders of eels infected with *A. crassus* were mostly moderate to low, a negative effect on the fitness of eels cannot be excluded. The unique spawning migration, a distance of almost 5000 km to the Sargasso Sea, requires maximum fitness and health. *Anguillicola crassus* was equally regarded as a serious threat in *A. rostrata* following its first occurrence (Fries *et al.*, 1996) in American brackish and fresh-water habitats, where infestation rates can now be up to 90% (COSEWIC, 2006). Eels that stay in a purely marine environment

are obviously not at risk of infection by these neozoans and may therefore be favoured to reach their spawning grounds in good condition. The common practice of catching glass eels in river estuaries for unselective restocking of fresh-water systems all over Europe might therefore worsen the problem of declining eel stocks by further diluting the number of eels that would stay in marine coastal habitats. Moreover, uncontrolled restocking further intensifies the risk of transferring diseases and parasites to pristine areas. This outcome has been demonstrated in a long-term study of eels in Swedish lakes and brackish waters in the spread of *A. crassus*; it was already well established in all localities investigated just 9 years after its first record in 1987 (Wickström *et al.*, 1998). For *A. rostrata* in Canadian waters, where *A. crassus* has not yet been detected, its arrival is seen as just a matter of time (COSEWIC, 2006).

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