

Effects of small weirs on fish parasite communities

Geraldine Loot · Yorick Reyjol · Nicolas Poulet ·
Andrea Simkova · Simon Blanchet · Sovan Lek

Received: 28 February 2007 / Accepted: 8 June 2007
© Springer-Verlag 2007

Abstract In this study, we examined the impacts of small weirs on the parasite community of gudgeon and toxostome in a medium-sized river. We tested changes on parasite species diversity using indices that capture both richness and abundance characteristics, and we examined parasite community structure with null models (co-occurrence index *C* score) and a multiple discriminant function analysis (MDFA). Our results showed that parasite community diversity of gudgeon is strongly influenced by weirs with a maximum diversity upstream of the weirs. Weirs also induce change in abundance of gudgeon parasite species particularly during summer. Nevertheless, we obtained that weirs had no effect on the parasite co-occurrence patterns. In addition, similarity indices indicate that the parasite faunas of newly

established limnophilic species (roach and bleak) are host-specific and are rarely transmitted to other fish species. We conclude that fish parasite communities responded in different ways to the presence of impassable weirs, but, in a general tendency, changing environmental conditions induced by weirs may represent an ecological risk.

Introduction

Either due to anthropogenic effects or natural patchiness, habitat fragmentation in streams and rivers affects abiotic hydrographic parameters (Walker and Thoms 1993; Nilsson et al. 2005), aquatic organisms (Fahrig 2003) and has become a major concern in conservation biology. Because fish are dependent on the hydrographical networks of drainage basins and essentially disperse by fluvial corridors, conservation efforts have notably been investigated for them (e.g. Morita and Yamamoto 2002; Wofford et al. 2005). River fragmentation causes fast and deep modifications of fish communities (see Rosenberg et al. 1997 for a detailed review).

River fragmentation usually refers to the presence of one or successive dams (i.e. the “serial discontinuity concept”, Ward and Stanford 1983). Another type of widespread fragmentation—but very sparsely studied—is the river interruption by weirs. Weirs are usually smaller than hydroelectric dams, but more numerous in rivers catchments, and several studies have shown that they also cause severe impacts on habitat and their associated fish communities (Ovidio and Philippart 2002; Meldgaard et al. 2003; Baumgartner 2007).

Up until now, the effects of environmental changes induced by weirs have never been assessed on fish parasite communities. However, the effect of changing host envi-

G. Loot (✉) · S. Blanchet · S. Lek
Laboratoire Evolution et Diversité Biologique, U.M.R. 5174,
CNRS–Université Paul Sabatier,
118 route de Narbonne,
31062 Toulouse Cedex 4, France
e-mail: loot@cict.fr

Y. Reyjol
Département de Chimie-Biologie,
Université du Québec à Trois-Rivières,
C.P. 500, Trois-Rivières,
Quebec G9A 5H7, Canada

N. Poulet
Conseil Supérieur de la Pêche,
112 faubourg de la Cueille,
86000 Poitiers, France

A. Simkova
Department of Botany and Zoology, Faculty of Science,
Masaryk University,
Kotlářská 2,
61137 Brno, Czech Republic

ronmental conditions on parasite communities has recently received increasing attention (Barger and Esch 2001; McCallum and Dobson 2002). Fish parasite communities may provide important information on ecosystem conditions due to their intimate contact with both the host and aquatic environments (Kadlec et al. 2003). Therefore, numerous authors concluded that parasite assemblages should be considered not only for their influence on fish health but also for their own changes in prevalence, abundance and diversity in response to environmental stressors (Landsberg et al. 1998; Lafferty and Kuris 1999; Valtonen et al. 2003). The vast majority of these investigations have focused on the effects of water pollution (e.g. Khan and Thulin 1991; Poulin 1992; Valtonen et al. 2003; Sures 2003), floods (Kadlec et al. 2003), human predation (Loot et al. 2005) and species introduction (Torchin et al. 2003; Gozlan et al. 2005; Ishtiaq et al. 2006) on the parasites.

Taking into account the particular sensitivity of parasites to environmental alteration and host community changes, we hypothesise that weirs may influence the parasite communities. Indeed, by changing abiotic parameters (Walker and Thoms 1993), weirs may lead to an increase in the physiological stress of the host and make them more susceptible to parasite infection. In addition, parasites may also be sensitive to environmental parameter changes such as temperature, flow and/or oxygen level and suffer higher mortality (Esch et al. 1990). Weirs may also modify the community of intermediate and/or definitive hosts that are important to the completion of the parasite life cycle. Finally, by modifying habitat, weirs may facilitate the colonisation by limnophilic fish species, which may transfer their parasite faunas to the local fish (Torchin et al. 1996).

The aim of the present study was to determine whether construction of weirs induced a change in fish parasite community structure. To do so, we studied one of the most impounded rivers in the Southwest France, the Viaur River (52 weirs for a length of 169 km). We examined and compared diversity and structure patterns in the parasite communities of two eurytopic target fish species that were present both upstream and downstream of the weirs: gudgeon (*Gobio gobio*) and toxostome (*Chondrostoma toxostoma*). This comparison was done during winter and summer season and at two levels of biological organization, i.e. the component and the compound community. We also examined the parasite community of two limnophilic colonising species upstream of the weirs: roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*), and we verify whether parasites of these fish species extend their host range toward the two target fish species. We finally discussed the potential impact of weirs on fish parasite communities within the context of biological conservation.

Materials and methods

Study area and sampling sites

The Viaur River is located in the Adour-Garonne catchment (southwestern France; Fig. 1). This rain-fed stream has its source at an altitude of 1,090 m in the piedmont zone of the Massif Central mountains. The average annual water temperature is 12°C (range 2–24°C). The Viaur is a highly dammed river, with 52 weirs and five dams present along the river, i.e. one obstacle every 3 km. Many of these weirs have been built during the Middle Age and are nowadays out of order: Sluices are closed and water flows over the weir (in winter) or runs through a small gap.

We selected three localities (Ayres, Albinet and Bonnecombes along 15 km stream with similar water quality, Loot et al., unpublished data). These three localities presented similar morphodynamic and physical conditions and are characterised by the presence of one weir which isolated typical upstream conditions (i.e. high water depth and low water velocity) from typical downstream ones (i.e. low water depth and high water velocity; see Table 1). Because these three weirs were previously identified as impassable for fish, we considered two sites in each locality i.e. upstream and downstream of the weir: Ayres (sites 1

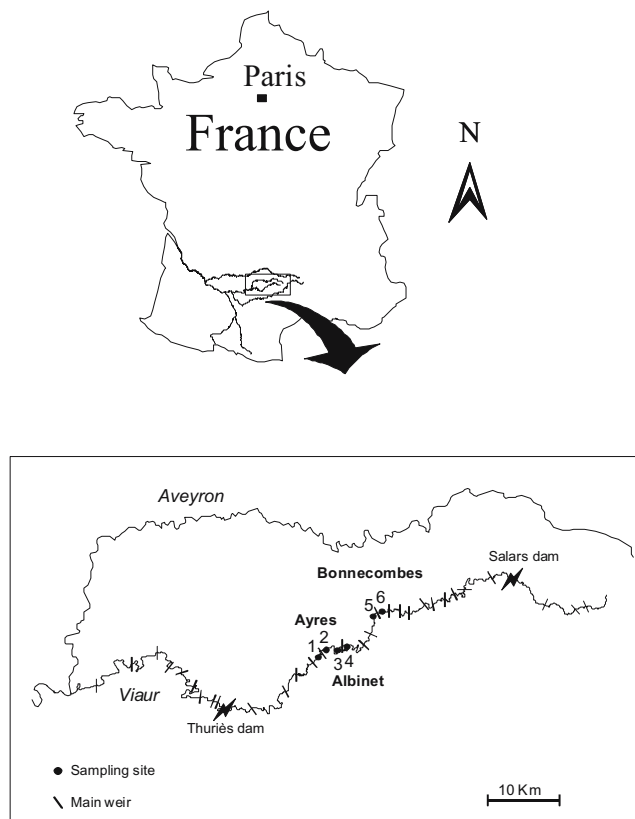


Fig. 1 Map of the Viaur River with the three localities: Ayres, Albinet and Bonnecombes and the six sampling sites upstream and downstream of the weirs. The lines indicate the position of the main weirs

Table 1 Environmental characteristics (temperature, velocity and depth), host species and sampled individuals with their total body size in each season upstream and downstream the weir

	Environmental characteristics			Host species	Number of individuals	Length of host fish mean±SD (mm)
	T (°C) mean±SD	Velocity (cm/s) range	Depth (cm) range			
Winter 2002						
Upstream	6.4±1.3	0–5	35–148	<i>Rutilus rutilus</i>	20	139.2±35.26
				<i>Alburnus alburnus</i>	16	136.9±25.01
				<i>Gobio gobio</i>	15	81.4±13.98
				<i>Chondrostoma toxostoma</i>	6	160.7±27.33
Downstream	6.3±1.3	5–105	10–54	<i>Gobio gobio</i>	17	99.2±12.21
				<i>Chondrostoma toxostoma</i>	10	149.0±23.11
Summer 2003						
Upstream	20.4±1.5	0–2	30–150	<i>Rutilus rutilus</i>	15	125.4±26.92
				<i>Alburnus alburnus</i>	11	119±26.93
				<i>Gobio gobio</i>	15	104.7±12.07
				<i>Chondrostoma toxostoma</i>	10	154.5±25.31
Downstream	20.6±1.6	3–96	8–46	<i>Gobio gobio</i>	15	109±12.16
				<i>Chondrostoma toxostoma</i>	9	127±14.30

and 2), Albinet (sites 3 and 4) and Bonnecombes (sites 5 and 6; Fig. 1). Mean temperature did not differ between localities and between upstream and downstream habitats (t test: $P>0.05$; Table 1).

Fish sampling

Fish were caught by electrofishing and net fishing over two seasons (winter: November 2002 and summer: July–August 2003), upstream and downstream of the weirs.

Upstream of the weirs, bleak (*A. alburnus* L.), roach (*R. rutilus* L.), toxostome (*C. toxostoma* Vallot) and gudgeon (*G. gobio* L.) dominated the host community. Downstream of the weirs, gudgeon, minnow (*Phoxinus phoxinus* (L.)) and toxostome dominated the community (Loot et al., unpublished data). Because gudgeon and toxostome were representative of both the upstream and the downstream part of the weirs, they were chosen as the two target species to study the parasite communities. Bleak and roach are two species that were greatly favoured by the construction of the weirs (due to the decrease of the flow and the increase in the water depth upstream of the weirs). Thus, the parasite community of these two species was analysed on the upstream part of the weir to verify whether they may have influenced the parasite community structure of gudgeon and toxostome.

For each sampling season, we collected five individuals from each target fish species (i.e. gudgeon and toxostome) at each locality and each habitat condition (upstream and downstream of the weir): Ayres (sites 1 and 2), Albinet (sites 3 and 4), Bonnecombes (sites 5 and 6; Fig. 1). In addition, five bleak and five roach were sampled at each season at each locality upstream of the weir. Sample size

was low because we did not want to alter local fish populations of the River Viaur. Indeed, *C. toxostoma* was referenced in the IUCN red list of threatened species. In the River Viaur, an important decline in toxostome abundance has occurred since the 1950s due to water pollution and dam construction (Poulet, personal communication). However, sample sizes were sufficient to estimate parasite community according to Koskivaara et al. (1991) and Halmetoja et al. (1992). To limit the effects of sampling heterogeneity, we collected fish during a short time span (15 days) and selected specimens with similar size (t test: $P>0.05$) between upstream and downstream habitats (Table 1).

Parasite community

Parasite collection

After capture, fish were immediately placed in a tank with original local water and transported alive to the laboratory. All fish were dissected in the following 24 h, and the following potential parasite habitats were examined: gills, fins, external body surface, eyes, body cavity, gonads, swim bladder, liver and intestine. All metazoan ectoparasites (Monogenea, Mollusca and Crustacea) and endoparasites (Digenea, Cestoda, Nematoda and Acanthocephala) were removed from each fish individual. Then, all specimens were identified to the species level using standardised protocols and adequate taxonomic determination handbooks: Gussev (1985) for *Dactylogyrus* and *Gyrodactylus*; Georgiev et al. (1986), Khalil et al. (1994) for Cestoda; Moravec (1994) for Nematoda and Fryer (1982) for Crustacea.

Parasite data analysis

Analyses of fish parasite diversity were carried out at the component community (all parasites in one fish species) and compound (all parasites in one locality) levels (see Holmes and Price 1986; Esch et al. 1990; Bush et al. 1997).

At the component community level, we first quantified two indices of diversity: numerical species richness and the Simpson's index which weight for abundance of the most common species (Magurran 2004). These indices were calculated at the individual level for gudgeon and toxostome, respectively. Individuals host that did not harbour any parasites were not considered for the calculation of the Simpson's index. These indices were compared using two-way analyses of variance (ANOVAs), with habitat (i.e. upstream or downstream of the weir) and season (i.e. winter or summer) as two fixed factors. We performed four independent ANOVA for the two target host species and the two indices, respectively.

Jaccard index of similarity (C_J) was used to assess qualitative similarity among component community of the different hosts:

$$C_J = \frac{a}{a + b + c}$$

with a =the total number of parasite species present in both samples, b =the number of parasite species present only in sample 1 and c =the number of parasite species present only in sample 2. Namely, upstream of the weirs, we compared the similarity between each transferred species (i.e. roach and bleak) and each target species (gudgeon and toxostome) to assess whether parasite exchange occurred among these species.

We compared the parasite community structure by quantifying co-occurrence patterns in each of the fish species (gudgeon and toxostome) between habitats (upstream and downstream of the weir) and season (winter and summer) using null models. The input matrix was the absence (0) or the presence (1) of a particular parasite species in a particular individual host (Connor and Simberloff 1979). We used the Stone and Roberts' (1990) C score metric as a quantitative index of community organisation. It is supposed to be robust to minor changes in community structure, resistant to type I error (Gotelli 2000), and C score represents one of the more powerful co-occurrence indices (Fellis et al. 2003). If this index is unusually large compared with a null distribution, pairwise species co-occurrence (segregation) is smaller than expected by chance. If the index is unusually small, the species co-occurrence (aggregation) is stronger than expected by chance. To assign the probability value to an observed C score, we used randomisation to construct a null distribution for the C score (Gotelli and Graves 1996). We selected the fixed-fixed algorithm (see Gotelli 2000 for more details) recently used by Gotelli and

Rohde (2002), Mouillot et al. (2005) to study parasites communities of marine fishes. For each presence-absence matrix, we created 5,000 random matrices by reshuffling the elements of each row of the matrix. We then calculated the C score for each random matrix and estimated the tail probability (two-tailed test) of the observed matrix by comparing it with the histogram of simulated values. To test for differences in co-occurrence between upstream and downstream and winter and summer, we used a simple partition test as a null model (see Stone et al. 2000; Sanders et al. 2003 for more details). The observed variance in C scores between sample plots (upstream/downstream and winter/summer) was compared with the histogram of 5,000 variances created through random partitions of the data set.

At the compound community level, we performed a multiple discriminant function analysis (MDFA, Legendre and Legendre 1998) to test whether the four communities (i.e. downstream of the weirs in winter, downstream of the weirs in summer, upstream of the weirs in winter and upstream of the weirs in summer) significantly differed in regard to fish parasite abundances. MDFA is a method of linear modelling that aims to determine to what extent a set of quantitative descriptors (in our case, the parasite abundance in each fish) can explain a grouping that is known at the start of the analysis (in our case, the communities). To statistically test whether communities differed, we computed Monte-Carlo tests, which is a non-parametric version of the Pillai's test. As a complementary analysis, we performed an analysis of similarity (ANOSIM, Legendre and Legendre 1998) between each pair of community. ANOSIM provides a way to test whether there is a significant difference between two or more grouping units (in our case, the communities). If two groups of sampling units are really different in their species composition, then dissimilarities between the groups ought to be greater than those within the groups. Bray-Curtis index was used to assess dissimilarities among communities. The ANOSIM statistic (R) is based on the difference of mean ranks between groups and within groups. The statistical significance of observed R was assessed by permutation test. We applied Bonferonni correction to account for multiple comparisons.

Null model analyses were conducted with ECOSIM software v7.0 (Guild Structure option). The others statistics were performed using R version 2.2.1. (R Development Core Team 2005).

Results

Parasite community of investigated fish species

We found 22 species of parasites upstream of the weirs and 17 species downstream of the weirs. Results are detailed in

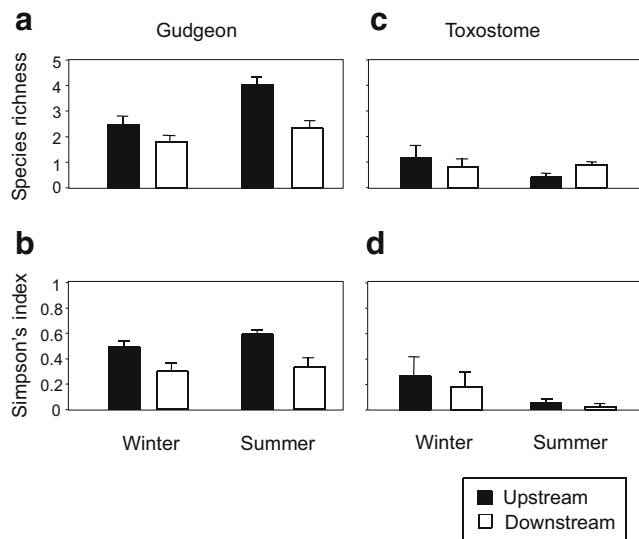


Fig. 2 The effect of the habitat (upstream vs downstream) and season (winter vs summer) on the parasite species richness (mean±SD) of gudgeon (a) and toxostome (c) and the parasite Simpson's index (mean±SD) of gudgeon (b) and toxostome (d)

Appendix, Table 5 (gudgeon), Appendix, Table 6 (toxostome), Appendix, Table 7 (roach) and Appendix, Table 8 (bleak).

Briefly, the parasite community of gudgeon was dominated by the two *Gyrodactylus* species, *G. markakulensis* and *G. gobii*. Toxostome possessed the lowest levels of epidemiological parameters (prevalence and intensity of infection). The maximum parasite intensity was recorded for the nematode *Rhabdochona denudata* (183 individuals per one fish) which dominated the parasite community of bleak.

Parasite diversity and dominance

Parasite species richness and Simpson's index for each fish species (gudgeon and toxostome) in each season and habitat

condition are represented in Fig. 2. Weirs influence the number of parasites harboured by the gudgeon (Table 2). Specifically, we found that for both season, the parasite species richness and the Simpson's index were higher upstream of the weirs (see Fig. 2a and b). The number of parasite species significantly increased in summer for both habitat (see Table 2 and Fig. 2a and b). In contrast, the Simpson's index did not change between seasons (Table 2b). These trends were not observed for the toxostome. Indeed, habitat condition did influence neither the species richness nor the Simpson's index of parasite (Table 2, Fig. 2c and d). In the same way, season sampling did not affect the number of parasites harboured by the toxostome (Table 2, species richness). We found a marginal effect of season on the Simpson's index of parasite, with the index being higher in winter (Table 2, Simpson's index; Fig. 2d).

Parasite similarity

Measurement of Jaccard index of similarity indicated that gudgeon and toxostome ectoparasite community exhibited a very low similarity with the one of roach and bleak (<7%; Table 3).

Gudgeon and toxostome endoparasite community showed low levels of similarity with endoparasite community of roach and bleak (<30%; Table 3).

Parasite community structure

Examination of co-occurrence patterns revealed random and unstructured patterns for each habitat condition and sampling season (Table 4). Indeed, the observed SES of C score did not differ significantly from a mean of zero ($p > 0.05$). There were no significant differences in the co-occurrence patterns between seasons and habitat conditions ($p > 0.05$).

Table 2 Results of ANOVA used to evaluate the effect of the habitat (upstream vs downstream), season (winter vs summer) and the resulting interaction on the parasite species richness of gudgeon and toxostome and the parasite Simpson's index of gudgeon and toxostome

	Gudgeon			Toxostome		
	F value	df	P value	F value	df	P value
Species richness						
Habitat	15.69	1, 58	0.000	0.18	1, 32	0.674
Season	12.36	1, 58	0.001	0.69	1, 32	0.312
Habitat × Season	2.60	1, 58	0.112	2.00	1, 32	0.089
Simpson's index						
Habitat	15.87	1, 55	0.000	0.15	1, 18	0.706
Season	1.38	1, 55	0.254	4.82	1, 18	0.041
Habitat × Season	0.35	1, 55	0.557	0.33	1, 18	0.572

P value<0.05 indicated significant effects.

Table 3 Jaccard index of similarity values (%) for endoparasite and ectoparasite assemblages between the four different fish species upstream the weir: roach, bleak, gudgeon and toxostome

Upstream	Ectoparasite	Endoparasite
roach–gudgeon	0	28.57
bleak–gudgeon	0	16.66
roach–toxostome	6.7	20
bleak–toxostome	0	25

Parasite compound community

According to the MDFA ordination, communities were significantly different (Monte-Carlo test; $p < 0.001$), with an explained inertia of 80% for the two first axes (axis 1, 45% and axis 2, 35%). Results of ANOSIM statistic test showed that weirs have a significant effect in summer ($p = 0.009$; comparison upstream vs downstream) and no effect in winter ($p = 0.525$; comparison upstream vs downstream). Concerning the season effect, we observed a significant effect upstream of the weirs ($p = 0.001$; for comparison winter vs summer) and downstream of the weirs ($p = 0.001$;

comparison winter vs summer). Consequently, we distinguished three communities (see Fig. 3):

- a winter community, dominated by *G. gobii*, highly gudgeon-specific
- a summer-downstream community dominated by *Lamproglena*, highly gudgeon-specific
- a summer-upstream community, characterised by *G. markakulensis*, highly gudgeon-specific

The impact of weirs is essentially observed on parasite community of gudgeon.

Discussion

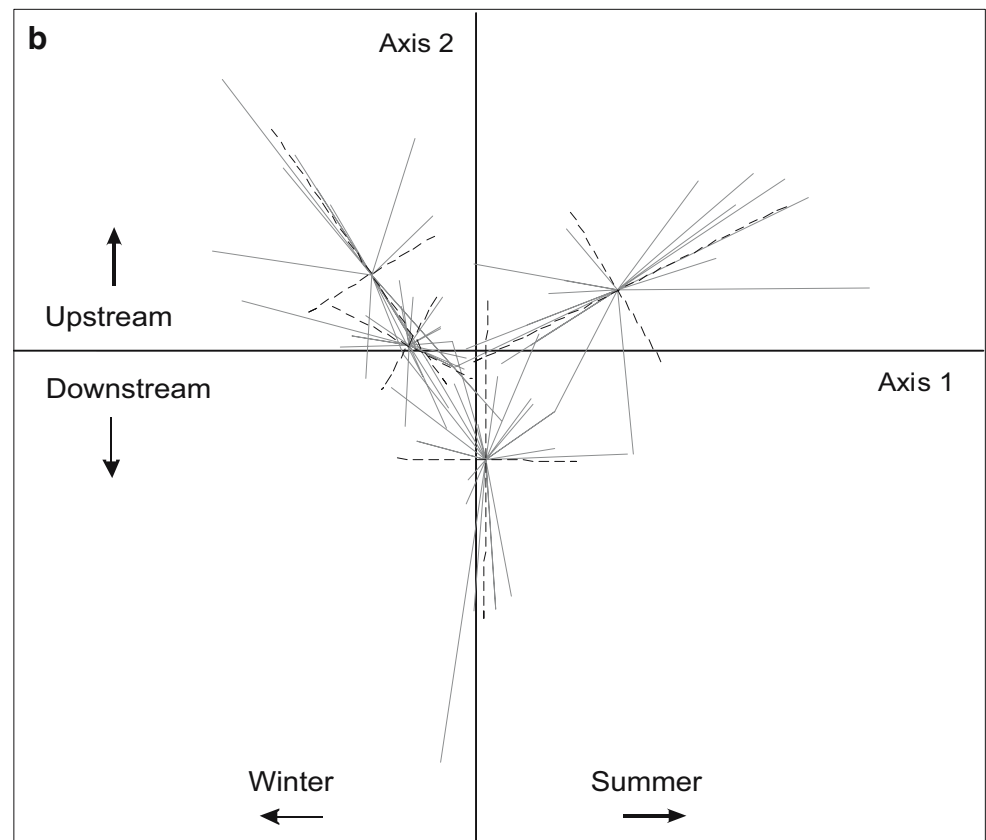
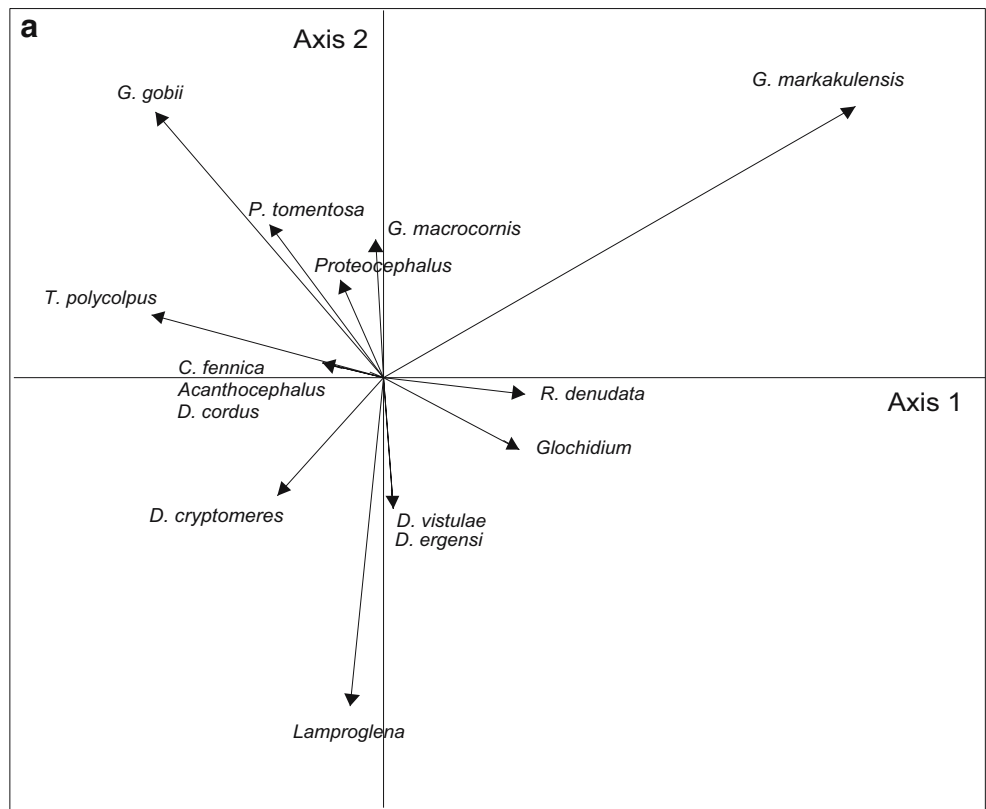
Our study demonstrated that human-induced fragmentation modifies the parasite community at both the component and compound levels. Specifically, we found that gudgeon harbours a parasite community that is more diverse upstream of the weirs. Moreover, the MDFA reveals that the parasite community of the Viaur River significantly differs between downstream and upstream of the weirs during the summer period.

Table 4 Summary of null models tests for fish parasite presence–absence matrices

	SES C score		p value
Gudgeon	Upstream winter	Upstream summer	Upstream winter/upstream summer
	0.47	−0.58	$p > 0.05$
	(random)	(random)	(no season effect)
	Downstream winter	Downstream summer	Downstream winter/downstream summer
	−0.32	0.02	$p > 0.05$
	(random)	(random)	(no season effect)
	Summer upstream	Summer downstream	Summer upstream/summer downstream
	−0.66	0.01	$p > 0.05$
(random)	(random)	(no locality effect)	
Toxostome	Winter upstream	Winter downstream	Winter upstream/winter downstream
	0.39	−0.30	$p > 0.05$
	(random)	(random)	(no locality effect)
	Upstream winter	Upstream summer	Upstream winter/upstream summer
	0.01	1.32	$p > 0.05$
	(random)	(random)	(no season effect)
	Downstream winter	Downstream summer	Downstream winter/downstream summer
	−0.49	0.01	$p > 0.05$
(random)	(random)	(no season effect)	
Toxostome	Summer upstream	Summer downstream	Summer upstream/summer downstream
	1.32	0.01	$p > 0.05$
	(random)	(random)	(no locality effect)
	Winter upstream	Winter downstream	Winter upstream/winter downstream
	0.01	−0.49	$p > 0.05$
	(random)	(random)	(no locality effect)

SES C score values are indicated for gudgeon and toxostome species upstream and downstream of the weirs during winter and summer periods. P value indicated the results of parasite community structure comparisons between the two localities (upstream and downstream) and the two seasons (winter and summer).

Fig. 3 Species (a) and samples (b) ordination biplots revealed by a multiple discriminant function analysis (MDFA). Parasites species not associated to an *arrow* correspond with species characterized by low abundances, which do not strongly contribute to community structuring



The maximum of parasite diversity observed for gudgeon upstream of the weirs may be explained by the prevailing environmental conditions (patterns of sediment transport, hydrologic variation, thermal and biological disruption; see Nilsson et al. 2005 for a review) which promote the simultaneous development of numerous parasite species. In contrast, the downstream conditions seem to favour the dominance of one or two species in the community. Alternatively, host species that colonised the sites upstream of the weirs, such as roach and bleaks, may have transported a subset of their “native” parasites to this new habitat (see Torchin et al. 2002; Prenter et al. 2004). For instance, Gozlan et al. (2005) demonstrated that the introduction of a new cyprinid fish *Pseudorasbora parva* had negative consequences on an endangered native fish *Leucaspis delineatus*. This threat was caused by the introduction of a highly non-specific pathogenic parasite. Nevertheless, in our study, we found that parasites infecting roach and bleak were specific and rarely transmitted to gudgeon and/or toxostome. We may notice that host specificity is most important for ectoparasites than for endoparasites. As endoparasites are ingested, they reflect the life habits of the fish, including prey interactions (Landsberg et al. 1998). Therefore, the composition of endoparasite communities could be related to the presence or absence of their larvae stages in the fish habitat. The high specificity of ectoparasites may be explained by the direct life cycle and their close physical contact with the host’s tegument and/or gills. Šimková et al. (2006) recognised that ectoparasites showed important morphological adaptations to survive on a particular host (e.g. attachment structures). Thus, the transmission of ectoparasites between native (i.e. gudgeon, toxostome) and newly established species (i.e. roach and bleak) was very limited.

M DFA analysis revealed differences in parasite communities between the sections upstream and downstream of the weirs, which was mainly due to the abundance of two parasite species. Indeed, *G. markakulensis* was dominant in the upstream-summer community, whereas *Lamproglena* was so in the downstream-summer community. The environmental conditions upstream of the weir (notably, low water velocities) may promote the life cycle dynamics of *G. markakulensis* (i.e. survival time, number of offspring) and/or the host activity, thus, increasing parasite transmission. We highlight that *Gyrodactylus* sp. may be a virulent pathogen inducing inflammatory reactions, particularly when fish suffer high parasite loads (Bakke et al. 1990). For instance, in Norwegian rivers, *G. salaris* was reported to be highly pathogenic, inducing a serious decrease of Atlantic salmon parr density during an epidemic (Olstad et al. 2006). Consequently, special emphasis and attention must be devoted to the potential impact of weirs, increasing abundance of such pathogenic parasites.

In addition to the effect of the weirs, parasite diversity of gudgeon was influenced by season, with parasite diversity being higher during summer. This result is explained by changes in water temperature along the seasonal gradient. Indeed, numerous parasite life cycles, through developmental stage, are affected by changes in temperature (Salvati et al. 2002; Cattadori et al. 2005). Specific to monogeneans, high water temperature was shown to increase *Dactylogyrus* sp. abundance (Koskivaara 1992). Alternatively, parasite assemblages could also be affected by seasonal host movements (spawning movements for instance), increasing the degree of the host’s social interactions and, consequently, the probability of parasite transmission (Karvonen et al. 2005). Although these seasonal changes in parasite communities have already been demonstrated in previous studies, they provide crucial information about the magnitude of the changes induced by weirs.

In contrast with gudgeon, toxostome were not affected by the presence of weirs and were weakly affected by seasons, suggesting that the parasite community of toxostome is more resilient to habitat conditions. These results are probably not attributable to the low parasite species richness and abundance the toxostome harboured, as we detected a weak but significant effect of the season.

Finally, our results revealed unstructured hierarchical patterns in parasite communities for the different seasons and habitat conditions. Null models of species association have recently proven to be useful to detect non-random patterns of co-occurrences in parasite communities and to infer the action of several structuring processes, such as competition (Poulin and Valtonen 2002; Fellis et al. 2003). Our findings suggest that antagonist interaction (competition) and/or positive association (aggregation) did not occur in fish hosts (Guégan and Huguény 1994). The lack of co-occurrence is likely to be the result of the low parasite species richness and abundance that have prevented the saturation of ecological niches. As a consequence, the interspecific interaction between parasites remains a rare phenomenon (Cornell 1993; Gotelli and Rohde 2002). Indeed, the parasite communities observed in the Viaur River have low levels of species richness and relative abundances compared to other European rivers (Šimková et al. 2001; Kadlec et al. 2003), which may be related to the high level of eutrophication of the Viaur River (Guilmet 1997; Sidall et al. 1997).

To conclude, the presence of weirs evidently disturbs the stream environmental characteristics and promotes the establishment of limnophilic fishes in the section upstream of the weirs. We hypothesise that the translocation of these species biologically and ecologically different (diet, size, microhabitat) from native fluvial fishes does not represent a potential risk for fish communities. Indeed, Euzet and Combes (1980) suggested that parasites could switch

between phylogenetically related hosts (usually within the same genus or family). Translocated and native species were phylogenetically different and so represent different habitat conditions for parasites, which may limit the rate of parasite transmission between them. In our view, the introduction of exotic species closely related to native species in non-altered fluvial habitats may be more dangerous and leads to the transmission of new parasites, as previously demonstrated by Fernando (1991) and Gozlan et al. (2005).

Nevertheless, in our study, we found that the relative diversity and abundance of several parasite species may be modified by the environmental conditions occurring upstream of the weirs. We demonstrated that according to the host species we considered, parasite communities responded in different ways to the presence of weirs. We therefore highlight the need to consider a large panel of host species when studying the effect of environmental

changes on parasite communities. However, we would like to note that our study has considered relatively few fish over 1 year, and it is therefore possible that additional differences have been undocumented. Ultimately, the full impact of weirs on fish parasite communities needs further elucidation, and we hope this study serves to emphasise the focus of future studies.

Acknowledgements AŠ was founded by the Research Project of Masaryk University, Brno, Project N.: MSM 0021 622 416. This manuscript was much improved by the comments of Robert Poulin. We are grateful to David J. Paž and Candida Shinn for correcting the English. We would like to thank Milan Gelnar, Boena Koubková and Markéta Ondraěková, (Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic) and Salah Bouamer (Centre de Biologie et Gestion des Populations, Campus international de Baillarguet, Montpellier, France) for their help with parasite determination. We are in debt to Fabien Leprieur who helped us in statistical analyses.

Appendix

Table 5 Parasite species communities of gudgeon in each season upstream and downstream the weir

	Parasite group	Winter 2002						Summer 2003					
		Upstream the weir			Downstream the weir			Upstream the weir			Downstream the weir		
		Prevalence	Intensity		Prevalence	Intensity		Prevalence	Intensity		Prevalence	Intensity	
		(%)	Mean	Min–Max	(%)	Mean	Min–Max	(%)	Mean	Min–Max	(%)	Mean	Min–Max
Ectoparasites													
<i>Dactylogyrus cryptomerus</i>	Monogenea	20	1.66	0–2	23.5	1.25	0–1	26.6	1.5	0–3	40	1.66	0–3
<i>Dactylogyrus</i> spp.	Monogenea	6.6	1	0–1	–	–	–	–	–	–	–	–	–
<i>Gyrodactylus gobii</i>	Monogenea	80	10.9	0–35	82.35	3.14	0–8	80	2.25	0–5	26.6	3	0–4
<i>Gyrodactylus markakulensis</i>	Monogenea	26.6	1.25	0–2	11.7	2	0–2	100	9.2	1–21	53.3	2.6	0–6
<i>Lamproglana pulchella</i>	Copepoda	20	2	0–3	11.7	7	0–11	26.6	1.75	0–3	66.6	6.8	0–18
<i>Tracheliastes polycolpus</i>	Copepoda	33.3	2	0–3	5.8	1	0–1	26.6	1.5	0–2	6.6	1	10–1
Endoparasites													
<i>Caryophyllaeides fennica</i>	Cestoda	–	–	–	5.8	1	0–1	–	–	–	–	–	–
<i>Rhabdochona denudata</i>	Nematoda	–	–	–	–	–	–	26.6	2	0–2	13.3	2	0–3
<i>Pseuicapillaria tomentosa</i>	Nematoda	6.66	1	0–1	5.8	1	0–1	–	–	–	–	–	–
<i>Acanthocephalus</i> spp.	Acanthocephala	–	–	–	5.8	2	0–2	–	–	–	–	–	–

Prevalence (%) and intensity of infection (mean) are indicated by each parasite species.

Table 6 Parasite species communities of toxostome in each season upstream and downstream the weir

	Parasite group	Winter 2002						Summer 2003					
		Upstream the weir			Downstream the weir			Upstream the weir			Downstream the weir		
		Prevalence	Intensity		Prevalence	Intensity		Prevalence	Intensity		Prevalence	Intensity	
		(%)	Mean	Min–Max	(%)	Mean	Min–Max	(%)	Mean	Min–Max	(%)	Mean	Min–Max
Ectoparasites													
<i>Dactylogyrus ergensi</i>	Monogenea	–	–	–	–	–	–	–	–	–	10	1	0–1
<i>Dactylogyrus vistulae</i>	Monogenea	–	–	–	–	–	–	–	–	–	10	1	0–1
<i>Dactylogyrus cordus</i>	Monogenea	16.6	1	0–1	20	1	0–1	–	–	–	–	–	–
<i>Gyrodactylus gobii</i>	Monogenea	16.6	2	0–2	–	–	–	–	–	–	–	–	–
<i>Gyrodactylus markakulensis</i>	Monogenea	16.6	1	0–1	–	–	–	–	–	–	–	–	–
<i>Gyrodactylus macrocornis</i>	Monogenea	16.6	2	0–2	–	–	–	10	1	0–1	–	–	–
Glochidium spp.	Lamellibranchiata	–	–	–	–	–	–	20	1.5	0–2	30	1.3	0–2
<i>Tracheliaestes polycolpus</i>	Copepoda	33.3	3	0–4	40	6	0–11	10	1	0–1	20	2.5	0–3
Endoparasites													
<i>Rhabdochona denudata</i>	Nematoda	–	–	–	20	8	0–13	–	–	–	10	1	0–1
<i>Proteocephalus</i> spp.	Cestoda	16.6	6	0–6	–	–	–	–	–	–	–	–	–

Prevalence (%) and intensity of infection (mean) are indicated by each parasite species. Larv. indicates that only larval stage of the parasite was found.

Table 7 Parasite species communities of roach in each season upstream the weir

	Parasite group	Winter 2002			Summer 2003		
		Upstream the weir			Upstream the weir		
		Prevalence	Intensity		Prevalence	Intensity	
		(%)	Mean	Min–Max	(%)	Mean	Min–Max
Ectoparasites							
<i>Dactylogyrus crucifer</i>	Monogenea	40	1.37	0–2	93.3	18	0–31
<i>Dactylogyrus nanus</i>	Monogenea	5	1	0–1	93.3	4.71	0–10
<i>Dactylogyrus caballeroi</i>	Monogenea	–	–	–	13.3	1	0–1
<i>Dactylogyrus rutili</i>	Monogenea	–	–	–	13.3	1	0–1
<i>Dactylogyrus sphyrna</i>	Monogenea	–	–	–	40	1	0–1
<i>Dactylogyrus suecicus</i>	Monogenea	–	–	–	26.6	1	0–1
<i>Gyrodactylus vimbi</i>	Monogenea	15	1	0–1	–	–	–
<i>Gyrodactylus</i> spp.	Monogenea	50	2	0–5	–	–	–
Glochidium spp.	Lamellibranchiata	–	–	–	6.6	2	0–2
Endoparasites							
<i>Caryophyllaeides fennica</i>	Cestoda	10	1	0–1	–	–	–
<i>Caryophyllaeides</i> larv. sp.	Cestoda	5	3	0–3	–	–	–

Table 7 (continued)

	Parasite group	Winter 2002 Upstream the weir			Summer 2003 Upstream the weir		
		Prevalence (%)	Intensity Mean	Min–Max	Prevalence (%)	Intensity Mean	Min–Max
<i>Rhabdochona denudata</i>	Nematoda	10	1	0–1	26.6	1.5	0–2
<i>Philometra rischta</i>	Nematoda	10	2	0–3	–	–	–
<i>Raphidascaris acus</i>	Nematoda	–	–	–	6.6	1	0–1

Prevalence (%) and intensity of infection (mean) are indicated by each parasite species. Larv. indicates that only larval stage of the parasite was found.

Table 8 Parasite species communities of bleak in each season upstream the weir

	Parasite group	Winter 2002 Upstream the weir			Summer 2003 Upstream the weir		
		Prevalence (%)	Intensity Mean	Min–Max	Prevalence (%)	Intensity Mean	Min–Max
Ectoparasites							
<i>Dactylogyrus</i> spp.	Monogenea	6.2	1	0–1	–	–	–
<i>Gyrodactylus laevis</i>	Monogenea	6.2	1	0–1	9	1	0–1
<i>Gyrodactylus</i> spp.	Monogenea	12.5	1	0–1	9	1	0–1
Endoparasites							
<i>Caryophyllaeides</i> larv. spp.	Cestoda	12.5	1.5	0–2	–	–	–
<i>Rhabdochona denudata</i>	Nematoda	62.5	41.3	0–183	18.1	1	0–1
<i>Philometra rischta</i>	Nematoda	–	–	–	9	1	0–1

Prevalence (%) and intensity of infection (mean) are indicated by each parasite species. Larv. indicates that only larval stage of the parasite was found.

References

- Bakke TA, Jansen PA, Hansen LP (1990) Differences in the host resistance of Atlantic salmon, *Salmo salar* L., stocks to the monogenean *Gyrodactylus salaris* Malmber, 1957. *J Fish Biol* 37:577–587
- Barger MA, Esch GW (2001) Downstream changes in the composition of the parasite community of fishes in an Appalachian stream. *J Parasitol* 87(2):250–255
- Baumgartner LJ (2007) Diet and feeding habits of predatory fishes upstream and downstream of a low-level weir. *J Fish Biol* 70 (3):879–894
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revised. *J Parasitol* 83:547–583
- Cattadori IM, Haydon DT, Hudson J (2005) Parasites and climate synchronize red grouse populations. *Nature* 433:737–741
- Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition. *Ecology* 60:1132–1140
- Cornell HV (1993) Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA, pp 243–252
- Esch GW, Bush AO, Aho JM (1990) *Parasite communities: patterns and processes*. Chapman & Hall, London
- Euzet L, Combes C (1980) Les problèmes de l'espèce chez les animaux parasites. *Bull Soc de Zool Fr* 40:239–285
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Syst* 34:487–515
- Fellis KJ, Negovetich NJ, Esch GW, Horak IG, Boomker J (2003) Patterns of association, nestedness, and species co-occurrence of helminth parasites in the greater kudu, *Tragelaphus strepsiceros*, in the Kruger National Park, South Africa and the Etosha National Park, Namibia. *J Parasitol* 89:899–907
- Fernando CH (1991) Impacts of fish introduction in Tropical Asia and America. *Can J Fish Aquat Sci* 48(Suppl 1):24–32
- Fryer G (1982) *The parasitic copepoda and branchiura of British freshwater fishes. A handbook and key*. Freshwater Biological Association, The Ferry House, Ambleside, Cumbria, p 87
- Georgiev B, Biserkov V, Genov T (1986) In toto staining method for cestodes with iron acetocarmine. *Helminthologia* 23:279–281
- Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621
- Gotelli NJ, Graves GR (1996) *Null models in ecology*. Smithsonian Institution Press, VA
- Gotelli NJ, Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol Lett* 5:86–94

- Gozlan RE, St-Hilaire S, Feist SW, Martin P, Kent ML (2005) Disease threats on European fish. *Nature* 435:1003–1136
- Guégan JF, Huguény B (1994) A nested parasite species subset pattern in tropical fish: host as major determinant of parasite infracommunity structure. *Oecologia* 100:184–189
- Guilmet M (1997) Schéma départemental à vocation piscicole—Aveyron—Bassin du Viaur—Synthèse. pp 102. FDAAPPMA, Aveyron
- Gussev AV (1985) Key to parasite of freshwater fish of the USSR. Metazoan parasites, vol 2 (in Russian). Academy of Sciences, Leningrad
- Halmetoja A, Valtonen ET, Taskinen J (1992) Trichodinids (Protozoa) on fish from four Central Finnish lakes of differing water quality. *Aqua Fenn* 22:59–70
- Holmes JC, Price PW (1986) Communities of parasites. In: Kikkawa J, Anderson DJ (eds) *Community ecology: patterns and processes*. Blackwell Scientific Publications, Oxford, pp 187–213
- Ishtiaq F, Beadell JS, Baker AJ, Rahmani AR, Jhala YV, Fleischer RC (2006) Prevalence and evolutionary relationships of haematozoan parasites in native versus introduced populations of common myna *Acridotheres tristis*. *Proc R Soc Lond B* 273:587–594
- Kadlec D, Šimková A, Jarkovský J, Gelnar M (2003) Parasite communities of freshwater fish under flood condition. *Parasitol Res* 89:272–283
- Karvonen A, Cheng GH, Valtonen ET (2005) Within-lake dynamics in the similarity of parasite assemblages of perch (*Perca fluviatilis*). *Parasitology* 131:817–823
- Khalil LF, Jones A, Bray RA (1994) Keys to the cestode parasites of vertebrates. International Institute of Parasitology and Institute of CAB International, hardback, 768 pp
- Khan RA, Thulin J (1991) Influence of pollution on parasites of aquatic animals. *Adv Parasitol* 30:201–238
- Koskivaara M (1992) Environmental factors affecting monogeneans parasitic on freshwater fishes. *Parasitol Today* 8:339–342
- Koskivaara M, Valtonen ET, Prost M (1991) Dactylogyrids on the gills of roach in Central Finland: features of infection and species composition. *Int J Parasitol* 21:565–572
- Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnol Oceanogr* 44:925–931
- Landsberg JH, Blakesley BA, Reese RO, Mcrae G, Forstchen PR (1998) Parasites of fish as indicators of environmental stress. *Environ Monit Assess* 51(1–2):211–232
- Legendre P, Legendre L (1998) *Numerical ecology* (2nd English edn). Elsevier, Amsterdam
- Loot G, Aldana M, Navarrete S (2005) Marine protected areas and parasitism in intertidal food webs. *Conserv Biol* 19:203–212
- Magurran AE (2004) *Measuring biological diversity*. Blackwell Publishing, Malden, MA
- McCallum H, Dobson A (2002) Disease, habitat fragmentation and conservation. *Proc R Soc Lond B* 269:2041–49
- Meldgaard T, Nielsen EE, Loeschcke V (2003) Fragmentation by weirs in a riverine system: a study of genetic variation in time and space among populations of European grayling (*Thymallus thymallus*) in a Danish river system. *Conserv Genet* 4:735–747
- Moravec F (1994) Parasitic nematodes of freshwater fishes of Europe. Academia, Prague, 473 pp
- Morita K, Yamamoto S (2002) Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conserv Biol* 16:1318–1323
- Mouillot D, George-Nascimento M, Poulin R (2005) Richness, structure and functioning in metazoan parasite communities. *Oikos* 109:447–460
- Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. *Science* 308:405–408
- Olstad K, Cable J, Robertsen G, Bakke TA (2006) Unpredicted transmission strategy of *Gyrodactylus salaris* (Monogenea: Gyrodactylidae): survival and infectivity of parasites on dead hosts. *Parasitology* 133:33–41
- Ovidio M, Philippart JC (2002) The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia* 483:55–69
- Poulin R (1992) Toxic pollution and parasitism in freshwater fish. *Parasitol Today* 8:58–61
- Poulin R, Valtonen ET (2002) The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. *Int J Parasitol* 32:1235–1243
- Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. *Trends Ecol Evol* 19(7):385–390
- R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rosenberg DM, Berkes F, Bodaly RA, Hecky RE, Kelly CA, Rudd JWM (1997) Large-scale impacts of hydroelectric development. *Environ Rev* 5:27–54
- Salvati L, Bolognesi M, Ascenzi P (2002) Does inhibition of *Trypanosoma cruzi* key enzymes affect parasite life cycle and geographic distribution? *IUBMB Life* 53(1):45–47
- Sanders NJ, Gotelli NJ, Heller NE, Gordon DM (2003) Community disassembly by an invasive species. *Proc Natl Acad Sci USA* 100(5):2474–2477
- Sidall R, Koskivaara M, Valtonen ET (1997) *Dactylogyrus* (Monogenea) infections on the gills of roach (*Rutilus rutilus* L.) experimentally exposed to pulp and paper mill effluent. *Parasitology* 114:439–446
- Šimková A, Gelnar M, Sasal P (2001) Aggregation of congeneric parasites (Monogenea: *Dactylogyrus*) among gill microhabitats within one host species (*Rutilus rutilus*). *Parasitology* 123:599–607
- Šimková A, Verneau O, Gelnar M, Morand S (2006) Specificity and specialization of congeneric monogeneans parasitizing cyprinid fish. *Evolution* 60(5):1023–1037
- Stone L, Roberts A (1990) The checkerboard score and species distributions. *Oecologia* 85:74–79
- Stone L, Dayan T, Simberloff D (2000) On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. *Am Nat* 156:322–328
- Sures B (2003) Accumulation of heavy metals by intestinal helminths in fish: an overview and perspectives. *Parasitology* 126:S53–S60
- Torchin ME, Lafferty KD, Kuris AM (1996) Infestation of an introduced host, the European green crab, *Carcinus maenas*, by a symbiotic nemertean egg predator, *Carcinonemertes epialti*. *J Parasitol* 82(3):449–453
- Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. *Parasitology* 124:S137–S151
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- Valtonen ET, Holmes JC, Aronen J, Rautalahti I (2003) Parasite communities as indicators of recovery from pollution: parasites of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in Central Finland. *Parasitology* 126:S43–S52
- Walker KF, Thoms MC (1993) Environmental effects of flow regulation on the lower River Murray, Australia. *Regulated Rivers Research & Management RRRMEP* 8(1–2):103–119
- Ward JV, Stanford JA (1983) The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in the lotic ecosystems. In: Fontaine TD, Bartell SM (eds) *The dynamics of lotic ecosystems*. Ann Arbor Science, Michigan, pp 47–63
- Wofford JEB, Gresswell RE, Banks MA (2005) Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. *Ecol Appl* 15:628–637