

Upstream-downstream gradient in infection levels by fish parasites: a common river pattern?

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SUMMARY

Physical habitat structure can influence the distribution and abundance of organisms. In rivers, stream drift, a common process originating from the unidirectional water flow, favours the displacement and downstream dispersion of invertebrates. This process could also generate a gradient in infection levels, leading to decreasing numbers of parasites per host as one moves upstream from the river mouth. We tested this hypothesis using 4 trematode species infecting the fish *Gobiomorphus breviceps* in the Manuherikia River (New Zealand). We analysed the abundance of each trematode infrapopulation as a function of distance from the river junction and fish size by generalized linear models. Our results supported the existence of a longitudinal gradient in trematode abundance along the river with a decreasing downstream-to-upstream continuum. This applied to 3 out of the 4 trematode species studied, suggesting that this might be a common pattern in river populations. Thus, the unidirectional river flow and a major process like drift in lotic systems, that influences the dynamics and distribution of invertebrate hosts, can also affect trematodes. Host properties like habitat preference, and parasite traits, particularly those related to transmission mode can influence the strength of the observed gradient, as may other environmental and biotic factors.

Key words: trematode abundance, unidirectional river flow, infection patterns, disease, River Continuum Concept, freshwater, *Coitocaeum parvum*, *Telogaster opisthorchis*, *Stegodexamene anguillae*, *Apatemon* sp.

INTRODUCTION

Parasitic infections are non-randomly distributed in space (Ostfeld *et al.* 2005). For instance, physical habitat structure can influence the distribution and abundance of organisms, and thus affect interspecific interactions such as host-parasite associations (Sousa and Grosholz, 1990). Several illustrations can be found in the literature. Disease was influenced by altitude in amphibian-fungal disease (Pounds *et al.* 2006), patch size and connectivity in tick-borne disease (Allan *et al.* 2003), deforestation in mosquito-borne malaria (Molyneaux, 2002) and basin-shape in *Daphnia*-fungal disease (Hall *et al.* 2010). Lotic systems (rivers) are very particular ecosystems in that they have a dendritic shape and continuous unidirectional water flow. In any river, the physical properties change drastically from its source to its mouth in ways that could affect infection patterns. Several theories exist in river ecology to explain such changes. The River Continuum Concept (RCC) developed by Vannote *et al.* (1980) predicts the way

in which biotic changes occur longitudinally instream in accordance to downstream changes in hydrologic and geomorphic properties. On the other hand, discrepancies have been explained by considering alternative factors such as heterogeneity of habitats, stochastic disturbance and hierarchical scaling (e.g., Perry and Schaeffer, 1987; Townsend, 1989; Benda and Dunne, 1997; Gomi *et al.* 2002). Only a handful of studies have addressed spatial patterns of parasite distributions in rivers (e.g. Kennedy, 1990; Barker *et al.* 1996; Weichman and Janovy Jr, 2000; Barger and Esch, 2001; Kennedy, 2001; Barger, 2006; Loot *et al.* 2007), but mostly focused on the similarities and heterogeneities in richness and abundance at the component community and infracommunity levels. In addition to those, a few have focused on the environmental determinants of myxozoan infections such as sediment type, temperature and flow rate in salmonid whirling disease (e.g. Krueger *et al.* 2006; Hallett and Bartholomew, 2008). So far, very little is known about disease distribution in rivers and the processes and environmental factors structuring infection foci in these habitats. Such information will undoubtedly be valuable for disease risk assessment in freshwater ecosystems.

In a river, a common process originating from the unidirectional river flow, stream drift, causes the

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displacement and downstream dispersion of typically benthic invertebrates. This process could promote a gradient in infection levels, leading to decreasing numbers of parasites per host as one moves upstream from the river mouth, in 2 different ways. First, the constant unidirectional drift of small organisms downstream (see e.g. Müller, 1954; Waters, 1961; Hynes, 1970; Townsend and Hildrew, 1976; Elliott, 2003; Lagrue *et al.* 2011) should lead to both free-living infective stages (miracidia, cercariae) and small intermediate hosts harbouring parasites (e.g. metacercariae infecting benthic amphipods and snails carrying intramolluscan stages) invariably moving downstream. Along the river, drifting infected invertebrate hosts and free-living stages may encounter pools or still reaches to settle (Hynes, 1970) and successfully infect an available host; alternatively, they become food for other organisms or perish. There is evidence that acanthocephalan-infected amphipods have a higher tendency to enter into the drift (McCahon *et al.* 1991; Maynard *et al.* 1998). This means that not only infective stages are lost from upstream sites, but also that they may accumulate in downstream reaches, possibly leading to disproportionately high infection levels in downstream sites.

Second, upstream reaches consist of less stable populations that tend to have lower densities of several organisms like plankton (e.g. Greenberg, 1964; O'Farrell, 1993; with exceptions in large rivers, see Basu *et al.* 2000; Allan, 2007) and other invertebrates (e.g. Perry and Schaeffer, 1987; Milner *et al.* 2001), because of drift, of lower resources and primary productivity, of lower temperature, and of greater physical disturbances (higher current speed and shallower waters occur upstream) following the RCC. It is well known, from theoretical models (Anderson and May, 1978; May and Anderson, 1978) and from empirical studies (e.g. Arneberg *et al.* 1998; Morand and Poulin, 1998; Arneberg, 2001; Sures and Streit, 2001; Hansen and Poulin, 2006), that parasite transmission and abundance are strongly dependent on host density. Therefore, because of a decreasing downstream-to-upstream gradient in host density, we would also expect a parallel longitudinal gradient in infection levels along the river.

In this study we tested for the existence of a decreasing gradient in infection levels with increasing distance upstream by examining the abundance of 4 trematode species with different life histories that infect upland bully (*Gobiomorphus breviceps* (Stokell, 1939)), a native New Zealand fish, along a river.

MATERIALS AND METHODS

Host – parasite system

We studied 4 trematodes, *Coitocaecum parvum* Crowcroft, 1944 (Opecoelidae), *Apatemon* sp. Szidat,

1928 (Strigeidae), *Stegodexamene anguillae* Macfarlane, 1951 (Lepocreadiidae) and *Telogaster opisthorchis* Macfarlane, 1946 (Cryptogonimidae). All four share the same first intermediate host, the New Zealand mudsnail *Potamopyrgus antipodarum* (Gray, 1843), but thereafter follow different life-cycle pathways. Cercariae of *Coitocaecum parvum* leave the snail and crawl on the substrate to infect an amphipod [*Paracalliope fluviatilis* (Thomason, 1879)] as intermediate host. Later, infected amphipods are ingested by upland bully, which represents the definitive host. Cercariae of *Apatemon* sp., *Stegodexamene anguillae* and *Telogaster opisthorchis* all leave the snail host and swim to locate and infect the upland bully *via* skin penetration, where they encyst as metacercariae within internal tissues. Subsequently, these 3 species are transmitted by predation on infected bullies by definitive hosts. *Apatemon* sp. infects ducks (*Anas platyrhynchos*, Bronwen Presswell, *personal communication*) as definitive hosts whereas both *S. anguillae* and *T. opisthorchis* use eels (*Anguilla australis* and *A. dieffenbachii*; only the latter occurs in the studied river). The upland bully is a mostly territorial benthic fish (McDowall, 1990), such that their infection levels reflect local processes.

Study area, fish sampling and parasite collection

The Manuherikia River is a 7th order stream with an average discharge of 15 cumecs (m^3s^{-1}) and is a tributary of the Clutha River, the largest river in New Zealand in terms of volume (Murray, 1975). In August 2010, we sampled the lower section of the Manuherikia River (Fig. 1), along a ~70 km stretch downstream from Falls Dam. The altitude difference was 328 m from the junction with the Clutha River to the uppermost site (Table 1). Predominant sediment size changed from boulders and cobble (sites 10–7) to very coarse gravel with patches of fine gravel (sites 6–4), to fine gravel with patches of coarse gravel (sites 3–1). We sampled upland bully fish longer than 3 cm standard length (6–33 specimens per site) by electrofishing at 10 sites along the river numbered sequentially from downstream to upstream (Fig 1, see Table 1 for coordinates). After capture, the standard length of each fish was measured, and they were then euthanised by spinal cord severing, and frozen at -20°C . Fish were subsequently thawed and dissected for parasite recovery according to a standardized protocol. Briefly, the digestive tract, liver, gall bladder, spleen, kidney, mesenteric tissue, gonads and muscle tissue were examined under a stereomicroscope for parasites. *Coitocaecum parvum* was recovered from the intestine whereas metacercariae of the other 3 species (*Apatemon* sp., *S. anguillae* and *T. opisthorchis*) were recovered from the liver, mesenteric tissue, gonads and muscle. Geographical distances between sampling sites were measured as river distances using ArcGIS 9.3.

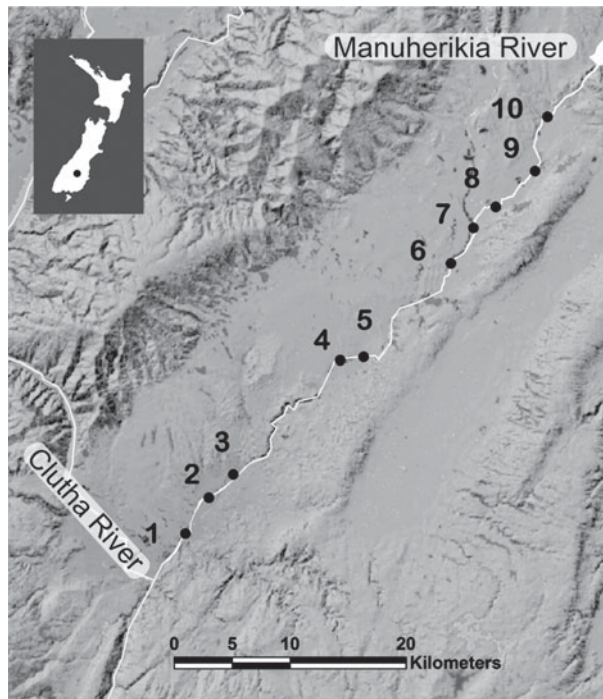


Fig. 1. Studied section of the Manuherikia River, and junction with the Clutha River, on the South Island (New Zealand), showing the 10 sampling sites numbered sequentially from downstream to upstream.

Statistical analyses

We tested whether fish size and fish sex ratio changed along the river using a linear regression and a χ^2 test, respectively. In order to test for accumulation of trematode infection in the lower sections of the river, generalized linear models (GLM) were performed with a negative binomial error structure fitting data on individual fish for each trematode species separately, using the abundance (number of parasites per host) of each species as the response variable. Trematode abundance data followed different distributions (either Gaussian or negative binomial) depending on the site along the river; however, the negative binomial provided the best fit to data pooled across all sites. As predictor variables the distance from the junction with the Clutha River (continuous variable), fish size (continuous variable) and the interaction fish size \times distance were used. Altitude was highly correlated with distance, therefore it was excluded from the analysis. For *Apatemon* sp. this analysis was run twice, including and excluding site 10 as it might represent an outlier influencing the result of the first analysis. An additional analysis including species as a factor was performed to test for the interaction species \times distance that would demonstrate different responses (different slopes for the relationship of abundance with distance) of the 4 species. All analyses were conducted in R freeware v. 2.13.1 (R Development Core Team, 2010), using the MASS, AED and CAR libraries (alpha = 0.05).

RESULTS

A total of 10 999 parasites were recovered from 131 fish along the river. *Coitocaecum parvum* reached the highest mean intensity in the river (50.3 ± 56.2 s.d.), followed by *Apatemon* sp. (42.1 ± 46.6 s.d.), *S. anguillae* (14.2 ± 22.4 s.d.) and *T. opisthorchis* (13 ± 16.7 s.d.). The most numerically dominant species (highest abundance) at sites 1, 3–4 was *C. parvum*, at sites 2, 5 and 10 it was *Apatemon* sp.; *T. opisthorchis* was dominant at sites 6–7, 9 whereas *S. anguillae* dominated at site 8. Fish size changed along the river ($R^2 = 0.090$; $F_{(1,129)} = 12.9$; $P < 0.001$), with larger fish occurring upstream. However, the relationship was not truly linear (Fig. 2), and is best described by a third-order polynomial regression ($R^2 = 0.236$; $F_{(3,127)} = 13.1$; $P < 0.001$), suggesting that still-water stretches or food abundance may not occur evenly along the river (a deep gorge exists between sampling sites 3 and 4). In contrast, sex ratio was similar ($\chi^2 = 18.58$; D.F. = 19; $P = 0.484$) among sites along the river.

Overall, increasing distance upstream had a negative effect on the abundance of 3 out of 4 parasite species (see Table 2 and Fig. 3). *Apatemon* sp. was the exception, with a negative effect of distance upstream only becoming apparent if the upstream-most site was removed from the analysis ($P < 0.001$; Table 2). Abundance dropped at site 6 and remained low further upstream in most cases (Fig. 3). Fish size had a positive statistically significant effect on infection levels for *T. opisthorchis* and *S. anguillae*, and *Apatemon* sp. when site 10 was ignored. The interaction fish size \times distance was not significant in any case (Table 2); whereas the interaction species \times distance was significant for all levels of the factor. Thus different trematode species showed slightly different abundance gradients with distance (Table 2; Fig. 3, note the different scale for the y-axes).

DISCUSSION

The goal of our study was to determine whether there was a gradient in the distribution of trematode abundance in a river. As predicted, our results supported the existence of such a longitudinal gradient in trematode abundance along the Manuherikia River with a decreasing downstream-to-upstream continuum. This result applied to 3 out of 4 different trematode species, suggesting that this might be a common pattern in river populations.

Multiple scenarios could explain a longitudinal infection gradient in rivers

In addition to the unidirectional water current favouring the dispersal and drift of organisms downstream, predicted changes in physical, chemical and biotic conditions along the length of a river following the RCC could in many ways contribute to

Table 1. Summary of sites and their characteristics for the fish parasite survey in the Manuherikia River: site coordinates, distance from the junction with the Clutha River, altitude, number of fish sampled, and mean fish size measured as standard length (and standard deviation) per site

Site	Coordinates (New Zealand Grid)	Distance (km)	Altitude (m)	No. of fish sampled	Fish size (cm; mean \pm s.d.)
1	E2229788; N5547804	5.520	150	9	3.9 \pm 0.7
2	E2231811; N5550908	9.960	164	11	4.5 \pm 0.5
3	E2233922; N5552927	13.320	173	6	3.8 \pm 0.6
4	E2243168; N5562780	29.950	303	13	4.3 \pm 0.8
5	E2245196; N5563056	32.670	256	6	3.8 \pm 0.6
6	E2252736; N5571134	45.000	367	11	4.9 \pm 0.7
7	E2254588; N5574660	50.120	389	25	5.6 \pm 1.0
8	E2256614; N5576034	53.669	410	8	5.0 \pm 1.1
9	E2260015; N5579132	59.283	437	9	4.9 \pm 1.2
10	E2261083; N5583837	64.834	478	33	4.6 \pm 0.8

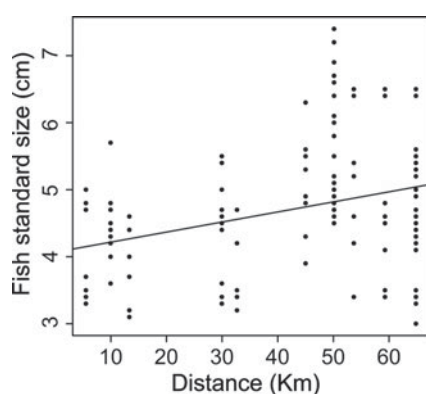


Fig. 2. Linear regression of standard length of upland bully, *Gobiomorphus breviceps*, as a function of distance from junction with the Clutha River.

the strength of the observed gradient in infection. For instance, a salinity and eutrophication gradient caused differences in parasite community structure, composition and abundance of some species between upstream and downstream sites in 2 polluted estuaries in Canada (Blonar *et al.* 2011). Other factors such as productivity, temperature, current speed, habitat or abundance of intermediate hosts could be influential in structuring infection foci in the Manuherikia River. Data from a study by the Otago Regional Council (2011) showed that median concentration of dissolved reactive phosphorus (DRP) was lowest upstream (corresponding to site 10 of the present study) and highest at Ophir (site 4). DRP increased towards downstream because it was not used in algal growth due to nitrogen limitations (Otago Regional Council, 2011). In the same study, water quality was rated as excellent in the upper sites and good from site 5 to downstream. Habitat in the main stem was graded as excellent at every site studied. Based on the above, physical and chemical conditions did not vary greatly in the \sim 70 km studied stretch. Indeed, DRP values (see Table 6 in Otago Regional Council, 2011) showed an average 4-fold increase from the uppermost (Loop road, site

10 in our study) to the most downstream site in the main stem (at Galloway, site 1 here) whereas mean trematode abundance increased 112-fold (*C. parvum*), 5-fold (*T. opisthorchis*) and 26-fold (*S. anguillae*) in the same \sim 70 km stretch studied. So, the increase in parasite abundance towards downstream was considerably larger than that of nutrients.

Biotic factors such as the presence of non-indigenous introduced trout (*Salmo trutta* L. and *Oncorhynchus mykiss* Walbaum 1792) could also contribute to the gradient. Kelly *et al.* (2009) showed that infection by *C. parvum*, *S. anguillae* and *T. opisthorchis* in upland bully was lower in those sites with high density of trout, through the so-called 'dilution' effect (loss of infective stages via penetration of non-suitable hosts), in tributaries of the Manuherikia River. The main stem is used by adult trout and includes also spawning and juvenile habitats. If a downstream-to-upstream gradient in trout density existed, it would also contribute to the results observed. The dendritic nature of the river can be relevant too. For instance, tributary confluences could affect by themselves the connectivity, distribution and abundance of organisms and disease (see Campbell Grant *et al.* 2007; Carrara *et al.* 2012).

We cannot pinpoint which factors contributed to the observed gradient. However, changes in productivity, as well as succession in fish assemblages or in dominant species of the macroinvertebrate community may occur along the studied stretch of the river. In relation to the latter, epidemiological models assume that parasite transmission success depends on local host density (May and Anderson, 1978; Roberts *et al.* 2002) and there exist thresholds below which parasite transmission can be disrupted (see Krkosek, 2010). In the case of parasites with complex life cycles, several studies have shown that intermediate host densities are in most cases correlated with the abundance of parasites in the final hosts (e.g. Sures

Table 2. Summary of the statistical results for the Generalised Linear Models evaluating the effect of distance from the river mouth (junction with the Clutha River) and fish size on the abundance of four trematode species in the upland bully. A statistical summary of the interaction distance \times species for the analysis on pooled data (species as a factor) is also included.

Species	Variables	Coefficients	S.E.	z-value	P-value
<i>C. parvum</i>	Distance	-0.107	0.009	-12.181	<0.001*
	Fish size	0.174	0.158	1.100	0.271
	Distance \times Fish size	0.001	0.010	0.076	0.940
<i>Apatemon</i> sp. (including site 10)	Distance	-0.007	0.036	-0.212	0.832
	Fish size	-0.249	0.411	-0.606	0.546
	Distance \times Fish size	0.001	0.008	0.151	0.880
<i>Apatemon</i> sp. (excluding site 10)	Distance	-0.076	0.007	-9.560	<0.001*
	Fish size	0.400	0.139	2.876	0.004*
	Distance \times Fish size	-0.003	0.008	-0.392	0.695
<i>T. opisthorchis</i>	Distance	-0.051	0.006	-8.005	<0.001*
	Fish size	0.730	0.119	6.137	<0.001*
	Distance \times Fish size	0.011	0.007	1.573	0.116
<i>S. anguillae</i>	Distance	-0.068	0.005	-12.757	<0.001*
	Fish size	0.590	0.098	5.980	<0.001*
	Distance \times Fish size	-0.001	0.006	-0.207	0.826
Species as factor	Intercept	3.629	0.115	31.461	<0.001*
	Distance	-0.007	0.006	-1.247	0.212
	Distance \times Species (<i>C. parvum</i>)	-0.104	0.009	-12.019	<0.001*
	Distance \times Species (<i>S. anguillae</i>)	-0.057	0.008	-6.779	<0.001*
	Distance \times Species (<i>T. opisthorchis</i>)	-0.036	0.008	-4.341	<0.001*

and Streit, 2001; Hansen and Poulin, 2006; de Montaudouin and Lancelot, 2011). Therefore, the unidirectional river current in combination with a major process like invertebrate drift in lotic systems which influences the dynamics and distribution of invertebrate hosts could also have an effect on the trematodes exploiting them. We focus below on the processes behind the gradient but a corollary direction for future studies would be to disentangle the biotic, physical and chemical factors that may influence this gradient in infections under natural conditions.

Avian trematode, the exception to the pattern

The absence of a gradient in the abundance of *Apatemon* sp. (except when ignoring the uppermost site) is not surprising. Previous studies have demonstrated the influence of host dispersal ability on the distribution and genetic makeup of trematode parasites infecting mammals, fish and birds (Blouin *et al.* 1995; Criscione and Blouin, 2004; Prugnolle *et al.* 2005; Louhi *et al.* 2010; Blasco-Costa *et al.* 2012). In particular, Criscione and Blouin (2004) found that parasites using both freshwater and terrestrial hosts in their life cycle (allogenic parasites) had less structured populations and higher gene flow among

subpopulations than parasite species that used only freshwater hosts. Similarly, Louhi *et al.* (2010) found that avian parasite dispersal, mediated by definitive bird hosts, acts as the homogenizing force limiting genetic differentiation in the parasites. Our results suggest that although a decreasing trend in abundance can also be found in *Apatemon* sp. when excluding the uppermost site, it may be easily counteracted by local environmental factors (e.g. habitat suitability for the definitive host) or host traits (e.g. definitive host dispersal ability). Indeed, there is evidence (Marcogliese *et al.* 2001) that proximity to a bird definitive host colony and other habitat characteristics are positively associated with abundance of bird trematodes in the second intermediate host (the upland bully in this case). Thus, local factors and host traits may be the main players determining the abundance and distribution of *Apatemon* sp. and possibly other trematodes with allogenic life cycles in freshwater habitats. Generally, local factors are expected to alter the longitudinal gradients in rivers (see also *T. opisthorchis* at site 9; Fig. 3C).

Extent of the influence of drift

In our system, not only invertebrates (snails, amphipods and trematode free-living stages) can be

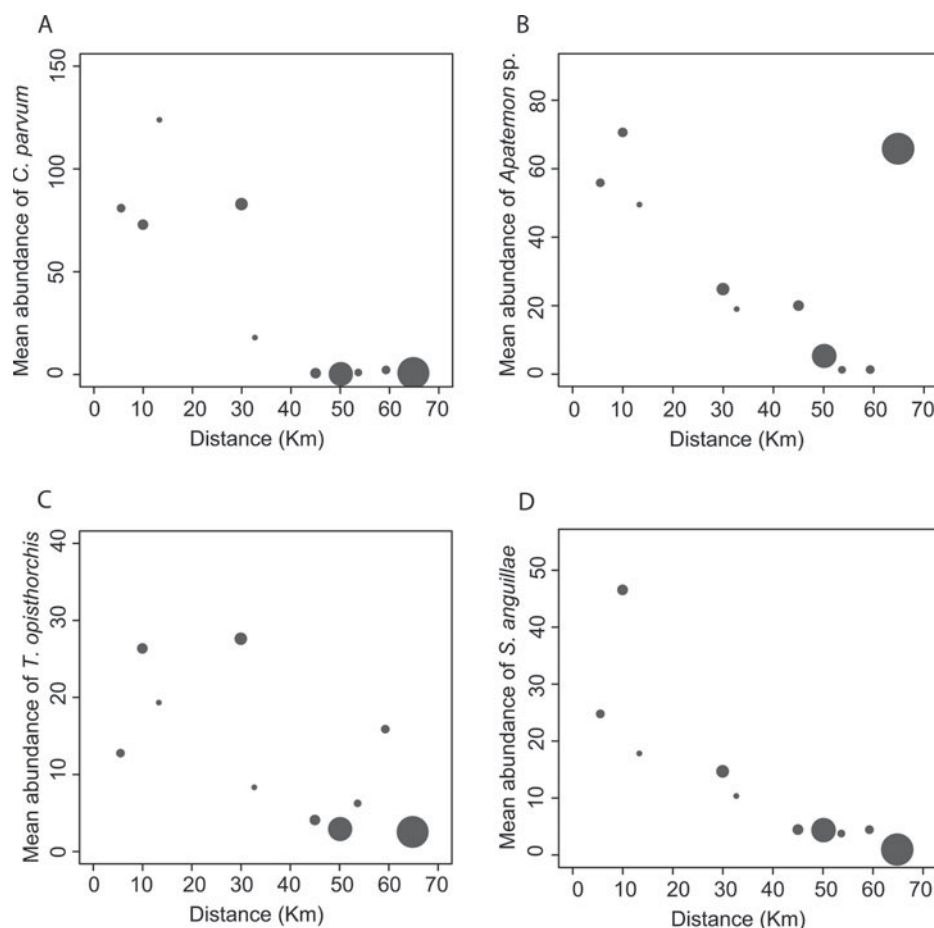


Fig. 3. Mean abundance of each trematode species per site *versus* distance from the downstream end of the river. (A) *Coitocaecum parvum*; (B) *Apatemon* sp.; (C) *Telogaster opisthorchis*; (D) *Stegodexamene anguillae*. Circle size is scaled to sample size. Note different scales of the y-axes.

subjected to drift. Hopkins (1970) reported that upland bully fry are passively dispersed downstream after hatching. After a couple of years, juvenile fish migrate upstream prior to establishing territories. The poor swimming ability of bully fry cannot prevent them from entering into drift, which should result in small or juvenile fish found more frequently downstream. Atkinson and Joy (2009) have shown that this is the case for an amphidromous New Zealand bully, *Gobiomorphus hubbsi* Stokell, 1959. Our results showed that upstream fish are, on average, a little larger than downstream ones, supporting Hopkins' (1970) observations on fry drift and adding a non-amphidromous species (although amphidromy is considered to be ancestral to all bully species in New Zealand) to the list of species with such behaviour. In addition, we found that fish size was positively correlated with abundance of both *T. opisthorchis* and *S. anguillae* (2 of the 5 trematodes found at the metacercarial stage, but also *Apatemon* sp. when site 10 was excluded). This agrees with previous studies showing that metacercariae accumulate in fish over time (Poulin, 2000). Despite upstream fish being larger and larger fish generally harbouring more *T. opisthorchis* and

S. anguillae, infection levels upstream were nevertheless lower.

The significance of invertebrate drift and unidirectional river current for parasites

Drift has been considered as being both beneficial (Hildrew and Townsend, 1980; Walton, 1980) and detrimental (Wooster, 1998) to benthic invertebrates. Cercariae of most trematode species live for only 1 or 2 days at most, under ideal laboratory conditions; under natural conditions, they are thus unlikely to infect hosts far downstream from their site of emergence from snails. Behavioural studies of parasitized invertebrates, typically amphipods, show that the behaviour of infected individuals is different from non-infected ones, showing a higher tendency for drifting caused by hyperactivity (McCahon *et al.* 1991; Maynard *et al.* 1998). The reason for such behaviour change is still debated (see McCahon *et al.* 1991; Jakobsen and Wedekind, 1998; Maynard *et al.* 1998; Wellnitz *et al.* 2003). In addition, acanthocephalans can cause spatial segregation of infected and uninfected subpopulations of an amphipod host (Wellnitz *et al.* 2003), with larger numbers of infected

amphipods drifting downstream and few moving upstream to compensate. Neither these authors nor Dezfuli *et al.* (1999) (who studied the same system) found a decreasing downstream-to-upstream pattern in infection (but the scale of their study was restricted to a 2 km stream section; see Dezfuli *et al.* (1999)). Since infected invertebrates tend to drift more and not all drifting infected invertebrates are caught by a fish predator, spatially structured host populations resulting from a 'parasite-induced drift' (Wellnitz *et al.* 2003) and regular drifting of free-living stages as a consequence of the unidirectional water current could also favour the establishment of higher infection areas in pools or still stretches downstream with higher host densities (also juvenile fish are more abundant downstream), where transmission is more likely. This could in turn favour genetic mixing within river populations with a higher genetic diversity downstream in those parasite species most influenced by invertebrate drift and river current dispersal (Blasco-Costa *et al.* 2012).

Host and parasite traits influencing an infection/abundance gradient

An additional question is to what extent such gradients in infection levels may be common to other parasitic groups, and what parasite and host traits may have an influence in addition to local environmental factors. As discussed above, dispersal ability of the definitive host (generally the most mobile in any trematode's life cycle) could alter the gradient. Other important host traits may include habitat preference (e.g. riffles *versus* backwaters, fast *versus* slow flows), feeding habits (e.g. filter-feeder *versus* detritivore *versus* active predator), or behaviour (e.g. gregarious *versus* solitary, territorial *versus* non-territorial). For example, *S. anguillae* and *T. opisthorchis* infecting eels as definitive hosts showed a similarly weak decrease in abundance with distance, whereas *C. parvum* that infects small territorial bully fish as definitive host showed a stronger effect.

Parasite traits, particularly those related to the life cycle, such as transmission mode and number of stages that entail suspension in the water column, could also influence the strength of the observed gradient. For instance, Cardon *et al.* (2011) investigated host and environmental features affecting the burden and pathogenicity of a copepod infecting its fish host. They found that the parasite burden along an upstream-to-downstream gradient was influenced by host factors, but not by environmental factors despite the target species being an ectoparasite. Most studies of parasites in fish with samples collected longitudinally in rivers involve pollution gradients (e.g. Krause *et al.* 2010; Marcogliese *et al.* 2009); therefore, they do not provide valid comparative estimates of infection gradients. We expect that this

longitudinal gradient in parasite abundance in rivers would exist also for other parasites with complex life cycles.

In summary, trematode abundance showed a longitudinal gradient, decreasing from downstream to upstream sites, and processes such as unidirectional water current and invertebrate drift that influence the distribution of invertebrates and juvenile fish inhabiting lotic systems could account for it. Other factors such as gradients in physical, chemical and biotic conditions along the stream could also contribute to explain the gradient. There is a need for further research to better understand the role of unidirectional water current, invertebrate drift and environmental factors as well as parasite and host traits in determining infection patterns and connectivity among parasite populations in river systems. Baseline knowledge on natural patterns in rivers is required in order to produce more accurate modelling of disease incidence and spread in freshwater ecosystems (Poulin *et al.* 2011; Thrush *et al.* 2011).

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REFERENCES

- Allan, B. F., Keesing, F. and Ostfeld, R. S. (2003). Effect of forest fragmentation on Lyme disease risk. *Conservation Biology* **17**, 267–272.
- Allan, J. D. (2007). *Stream Ecology*. Springer, London/New York.
- Anderson, R. M. and May, R. M. (1978). Regulation and stability of host-parasite population interactions. 1. Regulatory processes. *Journal of Animal Ecology* **47**, 219–247.
- Arneberg, P. (2001). An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* **24**, 352–358.
- Arneberg, P., Skorpung, A., Grenfell, B. and Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London, B*, **265**, 1283–1289.
- Atkinson, N. K. and Joy, M. K. (2009). Longitudinal size distributions of bluegill bullies (*Gobiomorphus hubbsi*) and torrentfish (*Cheimarrichthys fosteri*) in two large New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **43**, 643–651.
- Barger, M. A. (2006). Spatial heterogeneity in the parasite communities of creek chub (*Semotilus atromaculatus*) in southeastern Nebraska. *Journal of Parasitology* **92**, 230–235.
- Barger, M. A. and Esch, G. W. (2001). Downstream changes in the composition of the parasite community of fishes in an Appalachian stream. *Journal of Parasitology* **87**, 250–255.

- Barker, D. E., Marcogliese, D. J. and Cone, D. K. (1996). On the distribution and abundance of eel parasites in Nova Scotia: Local versus regional patterns. *Journal of Parasitology* **82**, 697–701.
- Basu, B. K., Kalfif, J. and Pinel-Alloul, B. (2000). Midsummer plankton development along a large temperate river: the St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 7–15.
- Benda, L. and Dunne, T. (1997). Stochastic forcing of sediment supply to channel networks from landsliding and debris flow. *Water Resources Research* **33**, 2849–2863.
- Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G. and Pollock, M. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. *Bioscience* **54**, 413–427.
- Blanar, C. A., Marcogliese, D. J. and Couillard, C. M. (2011). Natural and anthropogenic factors shape metazoan parasite community structure in mummichog (*Fundulus heteroclitus*) from two estuaries in New Brunswick, Canada. *Folia Parasitologica* **58**, 240–248.
- Blasco-Costa, I., Waters, J. M. and Poulin, R. (2012). Swimming against the current: Genetic structure, host mobility and the drift paradox in trematode parasites. *Molecular Ecology* **21**, 207–217.
- Blouin, M. S., Yowell, C. A., Courtney, C. H. and Dame, J. B. (1995). Host movement and the genetic structure of populations of parasitic nematodes. *Genetics* **141**, 1007–1014.
- Campbell Grant, E. H., Lowe, W. H. and Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**, 165–175.
- Cardon, M., Loot, G., Grenouillet, G. and Blanchet, S. (2011). Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: a multilevel causal analysis. *Journal of Animal Ecology* **80**, 657–667.
- Carrara, F., Altermatt, F., Rodriguez-Iturbe, I. and Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences, USA* **109**, 5761–5766.
- Criscione, C. D. and Blouin, M. S. (2004). Life cycles shape parasite evolution: Comparative population genetics of salmon trematodes. *Evolution* **58**, 198–202.
- de Montaudouin, X. and Lanceleur, L. (2011). Distribution of parasites in their second intermediate host, the cockle cerastoderma edule: Community heterogeneity and spatial scale. *Marine Ecology Progress Series* **428**, 187–199.
- Dezfuli, B. S., Rossetti, E., Bellettato, C. M. and Maynard, B. J. (1999). Pomphorhynchus laevis in its intermediate host *Echinogammarus stammeri* in the River Brenta, Italy. *Journal of Helminthology* **73**, 95–102, 130.
- Elliott, J. M. (2003). A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology* **48**, 1652–1668.
- Gomi, T., Sidle, R. C. and Richardson, J. S. (2002). Understanding processes and downstream linkages of headwater systems. *Bioscience* **52**, 905–916.
- Greenberg, A. E. (1964). Plankton of the Sacramento River. *Ecology* **45**, 40–49.
- Hall, S. R., Smyth, R., Becker, C. R., Duffy, M. A., Knight, C. J., MacIntyre, S., Tessier, A. J. and Cceres, C. E. (2010). Why are daphnia in some lakes sicker? disease ecology, habitat structure, and the plankton. *Bioscience* **60**, 363–375.
- Hallett, S. L. and Bartholomew, J. L. (2008). Effects of water flow on the infection dynamics of *Myxobolus cerebralis*. *Parasitology* **135**, 371–384.
- Hansen, E. K. and Poulin, R. (2006). Spatial covariation between infection levels and intermediate host densities in two trematode species. *Journal of Helminthology* **80**, 255–259.
- Hildrew, A. G. and Townsend, C. R. (1980). Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). *Animal Behaviour* **28**, 553–560.
- Hopkins, C. L. (1970). Some aspects of the bionomics in a brown trout nursery stream. *New Zealand Marine Department of Fisheries Research Bulletin* **4**, 38.
- Hynes, H. B. N. (1970). *The Ecology of Running Waters*, 1st Edn. Liverpool University Press, Liverpool, UK.
- Jakobsen, P. J. and Wedekind, C. (1998). Copepod reaction to odor stimuli influenced by cestode infection. *Behavioral Ecology* **9**, 414–418.
- Kelly, D. W., Paterson, R. A., Townsend, C. R., Poulin, R. and Tompkins, D. M. (2009). Has the introduction of brown trout altered disease patterns in native New Zealand fish? *Freshwater Biology* **54**, 1805–1818.
- Kennedy, C. R. (1990). Helminth communities in freshwater fish: structured communities or stochastic assemblages? In *Parasite Communities: Patterns and Processes* (ed. Esch, G. W., Bush, A. O. and Aho, J. M.), pp. 131–156. Chapman and Hall, London, UK.
- Kennedy, C. R. (2001). Metapopulation and community dynamics of helminth parasites of eels *Anguilla anguilla* in the River Exe system. *Parasitology* **122**, 689–698.
- Krause, R. J., McLaughlin, J. D. and Marcogliese, D. J. (2010). Parasite fauna of *Etheostoma nigrum* (Percidae: Etheostomatinae) in localities of varying pollution stress in the St. Lawrence River, Quebec, Canada. *Parasitology Research* **107**, 285–294.
- Krkosek, M. (2010). Host density thresholds and disease control for fisheries and aquaculture. *Aquaculture Environment Interactions* **1**, 21–32.
- Krueger, R. C., Kerans, B. L., Vincent, E. R. and Rasmussen, C. (2006). Risk of *Myxobolus cerebralis* infection to rainbow trout in the Madison River, Montana, USA. *Ecological Applications* **16**, 770–783.
- Lagrange, C., Kaldonski, N., Motreuil, S., Lefèvre, T., Blatter, O., Giraud, P. and Bollache, L. (2011). Interspecific differences in drift behaviour between the native *Gammarus pulex* and the exotic *Gammarus roeseli* and possible implications for the invader's success. *Biological Invasions* **13**, 1409–1421.
- Loot, G., Reyjol, Y., Poulet, N., Simkova, A., Blanchet, S. and Lek, S. (2006). Effects of small weirs on fish parasite communities. *Parasitology Research* **101**, 1265–1276.
- Louhi, K.-R., Karvonen, A., Rellstab, C. and Jokela, J. (2010). Is the population genetic structure of complex life cycle parasites determined by the geographic range of the most motile host? *Infection Genetics and Evolution* **10**, 1271–1277.
- Marcogliese, D. J., Compagna, S., Bergeron, E. and McLaughlin, J. D. (2001). Population biology of eye-flukes in fish from a large fluvial ecosystem: the importance of gulls and habitat characteristics. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **79**, 1102–1113.
- Marcogliese, D. J., Gendron, A. D. and Cone, D. K. (2009). Impact of municipal effluents and hydrological regime on myxozoan parasite communities of fish. *International Journal for Parasitology* **39**, 1345–1351.
- May, R. M. and Anderson, R. M. (1978). Regulation and stability of host-parasite populations interactions. 2. Destabilizing processes. *Journal of Animal Ecology* **47**, 249–267.
- Maynard, B. J., Wellnitz, T. A., Zanini, N., Wright, W. G. and Dezfuli, B. S. (1998). Parasite-altered behavior in a crustacean intermediate host: Field and laboratory studies. *Journal of Parasitology* **84**, 1102–1106.
- McCahon, C. P., Maund, S. J. and Poulton, M. J. (1991). The effect of the acanthocephalan parasite (*Pomphorhynchus laevis*) on the drift of its intermediate host (*Gammarus pulex*). *Freshwater Biology* **25**, 507–513.
- McDowall, R. M. (1990). *New Zealand Freshwater Fishes: A Natural History and Guide*. 2nd Edn. Heinemann Reed and Maf Publishing Group, Auckland, New Zealand.
- Milner, A. M., Taylor, R. C. and Winterbourn, M. J. (2001). Longitudinal distribution of macroinvertebrates in two glacier-fed New Zealand rivers. *Freshwater Biology* **46**, 1765–1775.
- Molyneux, D. H. (2002). Vector-borne infections and health related to landscape changes. In *Conservation medicine: Ecological Health in Practice* (ed. Aguirre, A. A., Ostfeld, R. S., Tabor, G. M., House, C. and Pearl, M. C.), pp. 194–206. Oxford University Press, Oxford, UK.
- Morand, S. and Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.
- Müller, K. (1954). Investigations on the organic drift in North Swedish streams. *Report of the Institute of freshwater research Drottningholm* **35**, 133–148.
- Murray, D. L. (1975). Regional hydrology of the Clutha River. *Journal of Hydrology (N.Z.)* **14**, 83–98.
- O'Farrell, I. (1993). Phytoplankton ecology and limnology of the Salado River (Buenos Aires, Argentina). *Hydrobiologia* **271**, 169–178.
- Ostfeld, R. S., Glass, G. E. and Keesing, F. (2005). Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* **20**, 328–336.
- Otago Regional Council (2011). *Water Quality and Ecosystem Health in the Manuherikia Catchment*. Otago Regional Council Technical Report. Otago Regional Council, Dunedin, New Zealand.
- Perry, J. A. and Schaeffer, D. J. (1987). The longitudinal distribution of riverine benthos: A river dis-continuum? *Hydrobiologia* **148**, 257–268.
- Poulin, R. (2000). Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *Journal of Fish Biology* **56**, 123–137.
- Poulin, R., Paterson, R. A., Townsend, C. R., Tompkins, D. M. and Kelly, D. W. (2011). Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. *Freshwater Biology* **56**, 676–688.
- Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sánchez-Azofeifa, G. A., Still, C. J. and Young, B. E. (2006). Widespread

- amphibian extinctions from epidemic disease driven by global warming. *Nature, London* **439**, 161–167.
- Prugnolle, F., Liu, H., De Meeùs, T. and Balloux, F.** (2005). Population genetics of complex life-cycle parasites: An illustration with trematodes. *International Journal for Parasitology* **35**, 255–263.
- R Development Core Team** (2010). *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roberts, M. G., Dobson, A. P., Arneberg, P., de Leo, G. A., Krecek, R. C., Manfredi, M. T., Lanfranchi, P. and Zaffaroni, E.** (2002). Parasite community ecology and biodiversity. In *The Ecology of Wildlife Diseases* (ed. Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H. and Dobson, A. P.), pp. 63–82. Oxford University Press, New York, USA.
- Sousa, W. P. and Grosholz, E. D.** (1990). The influence of habitat structure on the transmission of parasites. In *Habitat Structure: The Physical Arrangement of Objects in Space* (ed. Bell, S. S., McCoy, E. D. and Mushinsky, H. R.), pp. 300–324. Chapman and Hall, London, UK.
- Sures, B. and Streit, B.** (2001). Eel parasite diversity and intermediate host abundance in the River Rhine, Germany. *Parasitology* **123**, 185–191.
- Thrush, M. A., Murray, A. G., Brun, E., Wallace, S. and Peeler, E. J.** (2011). The application of risk and disease modelling to emerging freshwater diseases in wild aquatic animals. *Freshwater Biology* **56**, 658–675.
- Townsend, C. R.** (1989). The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**, 36–50.
- Townsend, C. R. and Hildrew, A. G.** (1976). Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* **45**, 759–772.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. and Cushing, C. E.** (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137.
- Walton, O. E.** (1980). Invertebrate drift from predator-prey associations. *Ecology* **61**, 1486–1497.
- Waters, T. F.** (1961). Standing crop and drift of stream bottom organisms. *Ecology* **42**, 532–537.
- Weichman, M. A. and Janovy Jr, J.** (2000). Parasite community structure in *Pimephales promelas* (Pisces: Cyprinidae) from two converging streams. *Journal of Parasitology* **86**, 654–656.
- Wellnitz, T., Giari, L., Maynard, B. and Dezfouli, B. S.** (2003). A parasite spatially structures its host population. *Oikos* **100**, 263–268.
- Wooster, D. E.** (1998). Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density. *Oecologia* **115**, 253–259.