

Research Paper

Cite this article: Paterson RA, Knudsen R, Blasco-Costa I, Dunn AM, Hytterød S, Hansen H (2019). Determinants of parasite distribution in Arctic charr populations: catchment structure versus dispersal potential. *Journal of Helminthology* **93**, 559–566. <https://doi.org/10.1017/S0022149X18000482>

Received: 25 February 2018

Accepted: 17 May 2018

First published online: 18 June 2018

Key words:

allogenic; autogenic; diversity; infracommunity; lentic; Norway; *Salvelinus alpinus*

Author for correspondence:

R.A. Paterson, School of Biosciences, Cardiff University, Cardiff CF10 3AX, UK
E-mail: patersonr3@cardiff.ac.uk

Determinants of parasite distribution in Arctic charr populations: catchment structure versus dispersal potential

R.A. Paterson¹, R. Knudsen², I. Blasco-Costa³, A.M. Dunn⁴, S. Hytterød⁵ and H. Hansen⁵

¹Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand; ²Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, Pb 6050 Langnes, 9037 Tromsø, Norway; ³Natural History Museum of Geneva, Malagnou Road 1, 1208 Geneva, Switzerland; ⁴School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK; and ⁵Norwegian Veterinary Institute, Pb 750 Sentrum, N-0106 Oslo, Norway

Abstract

Parasite distribution patterns in lotic catchments are driven by the combined influences of unidirectional water flow and the mobility of the most mobile host. However, the importance of such drivers in catchments dominated by lentic habitats are poorly understood. We examined parasite populations of Arctic charr *Salvelinus alpinus* from a series of linear-connected lakes in northern Norway to assess the generality of lotic-derived catchment-scale parasite assemblage patterns. Our results demonstrated that the abundance of most parasite taxa increased from the upper to lower catchment. Allogenic taxa (piscivorous birds as final host) were present throughout the entire catchment, whereas their autogenic counterparts (charr as final hosts) demonstrated restricted distributions, thus supporting the theory that the mobility of the most mobile host determines taxa-specific parasite distribution patterns. Overall, catchment-wide parasite abundance and distribution patterns in this lentic-dominated system were in accordance with those reported for lotic systems. Additionally, our study highlighted that upper catchment regions may be inadequate reservoirs to facilitate recolonization of parasite communities in the event of downstream environmental perturbations.

Introduction

Parasite distribution patterns are shaped by a suite of abiotic and biotic factors, which directly and/or indirectly influence both parasites and their hosts (Ostfeld *et al.*, 2005). In lotic-dominated freshwater ecosystems (i.e. rivers, streams), the combined influences of the unidirectional water flow and the mobility of the most mobile host are considered to be primary drivers structuring the distribution of parasites, especially those with complex life cycles (Blasco-Costa *et al.*, 2013; Salgado-Maldonado *et al.*, 2014). This often results in increased parasite richness and abundance in a downstream direction. However, the relative importance of such drivers in structuring parasite communities of catchments dominated by lentic environments (i.e. lakes, ponds) is poorly understood, as lentic environments are seldom compared along longitudinal gradients (i.e. upper to lower catchment, although see Valtonen *et al.*, 1997; Poulin and Valtonen, 2002).

Abiotic stability and persistence, both physical and chemical, vary considerably between lentic and lotic ecosystems (Jackson *et al.*, 2001), and thus the habitat available to both parasites and their hosts. The constant unidirectional water flow in lotic systems provides a mechanism for both free-living parasitic stages and infected hosts to disperse passively downstream, thus creating an environmental gradient of increasing infection from the upper to lower catchment (Blasco-Costa *et al.*, 2013). In contrast, standing waters provide limited opportunities for passive dispersal. Host mobility may play a greater role in determining how lentic-dominated catchment parasite communities are structured, as parasites utilizing a combination of aquatic and terrestrial hosts (e.g. birds, mammals; allogenic life cycle) have greater capabilities for dispersal than parasites remaining in aquatic environments throughout their life cycle (autogenic; Esch *et al.*, 1988).

Understanding the spatial structure of parasites and their hosts at a catchment scale has become increasingly important as researchers attempt to quantify the response of freshwater ecosystems to ever increasing environmental perturbations (e.g. Hofmann *et al.*, 2016). Whilst freshwater ecosystems are increasingly threatened by broad-scale stressors directly associated with climate change (e.g. reduced dissolved oxygen, increasing water temperature; Heino *et al.*, 2009; Woodward *et al.*, 2010), anthropogenic impacts on host–parasite interactions may be localized to the catchment or sub-catchment scale (e.g. point-source pollution,

© Cambridge University Press 2018. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

water impoundment; Morley, 2007; Oros and Hanzelová, 2009; Kelly *et al.*, 2010). Regardless of how such environmental perturbations arise, the absence of *a priori* knowledge in relation to host–parasite distribution in lentic-dominated catchments poses difficulties for quantifying parasite community impacts and recovery.

In this study we examined parasite distribution patterns in a lentic-dominated catchment in northern Norway, characterized by lake-specific populations of non-migratory Arctic charr *Salvelinus alpinus* (Præbel and Knudsen, 2012). This well-studied, cold-water specialist fish has diverse parasite assemblages (>20 parasite species in Norwegian freshwaters; Sterud, 1999), which differ greatly between populations and morpho-types (e.g. Skoglund *et al.*, 2015; Siwertsson *et al.*, 2016), thus making Arctic charr an excellent candidate to test catchment-scale parasite distribution hypotheses. In particular, we assessed charr–parasite distribution baselines in a watercourse consisting of a series of oligotrophic lakes at different altitudes. The catchment's potential resilience to parasite distribution against environmental disturbances was evaluated immediately prior to the application of rotenone, a pesticide highly toxic to freshwater fish, during a regional-scale eradication programme targeted towards the invasive salmon ectoparasite *Gyrodactylus salaris* (Hanssen, 2013).

The main aim of this study was to assess the generality of lotic-derived catchment-scale parasite assemblage patterns in lentic environments. First, we tested the overall hypothesis that parasite diversity increases in a downstream direction. Second, we assessed whether the mobility of the most mobile host determined species-specific parasite distribution patterns among lakes, independent of the upstream–downstream gradient. Specifically, we hypothesized that allogenic parasite taxa (i.e. parasites that utilized piscivorous birds as definitive hosts) would be more uniformly distributed within the catchment, whereas autogenic parasite taxa (i.e. non-migratory charr as definitive hosts) would have more restricted distributions. We also hypothesized that abundance patterns of allogenic parasites would be independent of the relative position of each lake in the catchment, whereas autogenic parasites would become increasingly abundant in a downstream direction (Blasco-Costa *et al.*, 2013).

Materials and methods

Study area

The Fusta catchment (544 km²), Nordland County, northern Norway comprises a series of linearly connected oligotrophic lakes: Luktvatnet (LV; 3.8 km², 137 m above sea level (masl)), Ømmervatnet (ØV; 5.6 km², 42 masl), Mjåvatnet (MV; 2.6 km², 39 masl) and Fustvatnet (FV; 10.6 km², 39 masl) (table 1, fig. 1). The uppermost lake, Luktvatnet, is connected to Ømmervatnet by the river Hattelva (8.0 km), with a small waterfall impeding upstream fish migration. Lakes Ømmervatnet and Mjåvatnet are connected by the river Straumanelva (1.8 km), whereas lakes Mjåvatnet and Fustvatnet are continuous apart from a short headland. Fustvatnet is connected to the Vefsn fjord by the Fusta river (8.5 km, total catchment length 56 km), where between 1880 and 1992 a fish ladder facilitated upstream migration of anadromous fish beyond a 10 m high waterfall on the river. The lower lakes (ØV, FV) are ice covered for approximately 5–6 months of the year, with the higher altitude Luktvatnet covered for an additional 4–5 weeks (Å. Kvambekk, pers. comm.; unpublished database of the Norwegian Water Resources and Energy Directorate). The

dominant catchment land use is native forest (pine/spruce; >80%), although there is a gradual downstream increase in modified agricultural land (LV, 2%; ØV, 10%; FV, 15%; NVE, 2015).

Fish communities in all lakes of the Fusta catchment consist primarily of Arctic charr, brown trout *Salmo trutta*, and three-spined stickleback *Gasterosteus aculeatus*. European eel *Anguilla anguilla* is rare in the system. Earlier, anadromous populations of Atlantic salmon *Salmo salar* and sea trout *S. trutta* could enter the lakes via a fish ladder in the Fusta river, but the ladder was closed in 1992 (Sæter, 1995).

Fish sampling

Arctic charr was selected as the focal fish species to assess parasite distribution patterns in a lentic-dominated catchment; charr have greater parasite diversity than other sympatric fish species (Knudsen *et al.*, 2008; Kristmundsson and Richter, 2009), and are represented by non-migratory populations in each lake in the study catchment (Præbel and Knudsen, 2012), thus providing an ideal system to test the influence of definitive host mobility on parasite distribution. To reduce potential variability in parasite assemblages as a result of differences in both diet and habitat associated with Arctic charr morph types (Skoglund *et al.*, 2015), this study examined the littoral spawning morph only. To reduce the potential effects of host age on parasite acquisition (Poulin, 2000), we primarily selected fish with fork length of 200–250 mm. Additionally, to reduce the total number of fish used in this research, we utilized specimens collected during a rotenone application at Ømmervatnet (n = 24) and Fustvatnet (n = 23) in October 2012, and by gill-netting lake margins of Luktvatnet (n = 24) in October 2013. Gill-netted fish were euthanized following the strict codes of practice in force in Europe and frozen at –20°C until parasitological examination. No approval from Institutional Animal Care and Use Committee (IACUC) or ethics committee was necessary. Mjåvatnet was excluded from our study as this shallow lake supported a very limited Arctic charr population (fig. 1).

Parasite collection and identification

Each fish was thawed, measured (fork length; mm) and weighed (g), before external surfaces (e.g. fins, gill opercula) were examined macroscopically for ectoparasites. The alimentary tract, eyes and gills were removed and systematically screened for parasites. Trematode eye flukes were identified to genus level only (i.e. *Diplostomum* sp. or *Tylodelphys* sp.), however previous research suggests the simultaneous occurrence of multiple lineages and/or species from each genus is likely in each Arctic charr host (e.g. Blasco-Costa *et al.*, 2014, 2017).

Data analyses

Component community (i.e. all parasites in the sampled Arctic charr in each lake, *sensu* Bush *et al.*, 1997) differences in parasite assemblages among lakes were assessed by calculating the taxa richness (total number of parasite taxa *S*) and Jaccard's index of community composition similarity ($S_j = c/(a + b + c)$), where *a* and *b* represent the number of taxa in lakes *a* and *b*, and *c* is the number of taxa common to both lakes. To assess infracommunity (i.e. all parasites in a single charr; Bush *et al.*, 1997) differences among lakes, we also calculated the number of taxa *S*, total abundance *N*, taxa diversity (Margalef's D_{Mg} ; Clifford and Stephenson, 1975) and evenness (Berger–Parker index *d*; Berger

Table 1. Characteristics of Arctic charr and the lakes from which they were sampled in the Fusta catchment, Nordland, Norway.

Lake	Sample year	Altitude (masl)	Area (km ²)	Depth (m)	Location	No. of charr	Fish length (mm), mean \pm SE ^a	Total weight (g), mean \pm SE ^b
Luktvatnet	2013	137	3.8	62	66°02'30.4"N 13°34'06.1"E	24	242.9 \pm 7.5	203.7 \pm 16.5
Ømmervatnet	2012	42	5.3	65	65°59'33.5"N 13°24'56.7"E	22	238.4 \pm 5.7	147.7 \pm 10.4
Fustvatnet	2012	39	10.6	65	65°54'20.7"N 13°23'28.6"E	23	253.9 \pm 7.4	190.4 \pm 17.6

^a No difference in fork length among lakes; one-way ANOVA $F_{2,66} = 1.28$, $P = 0.286$

^b Total weight differed between Luktvatnet and Ømmervatnet; one-way ANOVA $F_{2,66} = 3.59$, $P = 0.033$; Tukey HSD

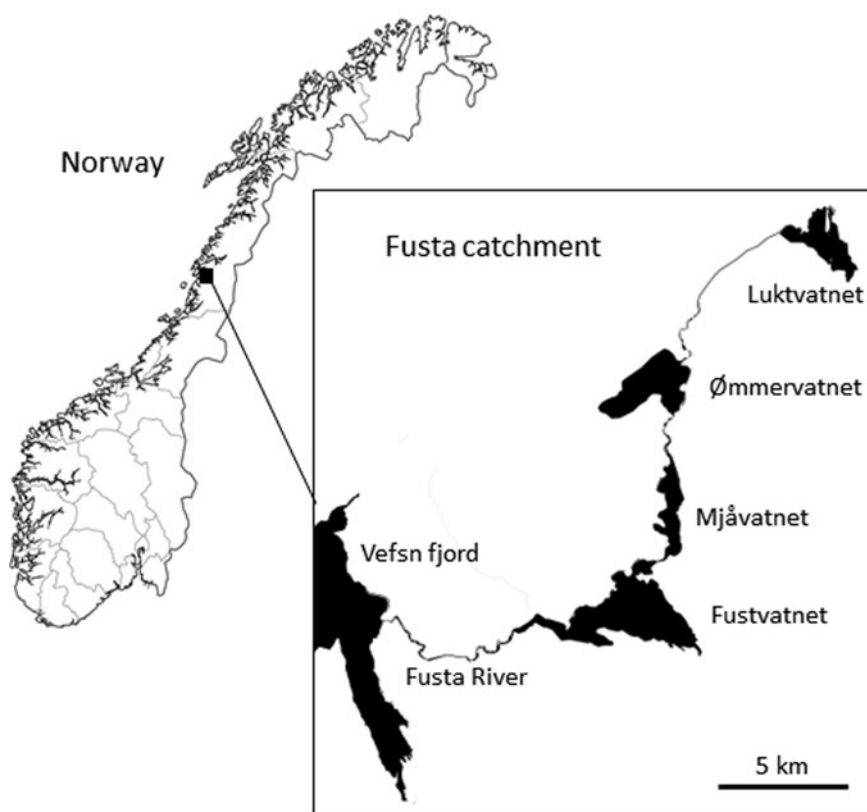


Fig. 1. Lakes Luktvatnet, Ømmervatnet, Mjåvatnet and Fustvatnet of the Fusta catchment, Nordland County, Norway.

and Parker, 1970) per charr. Although not frequently used in parasite ecology, the Margalef's diversity index provides stronger discriminatory abilities than other more commonly used indices (e.g. Shannon) by incorporating both individual and species abundance (Magurran, 2003).

All statistical analyses were computed using R v. 3.3.2 (R Development Core Team, 2016). Differences in number of taxa S , total abundance N , taxa diversity D_{Mg} and evenness d per charr among lakes were compared using separate general linear models (nlme::glm, version 3.1–131; Pinheiro *et al.*, 2017). Differences in the abundance of each parasite taxon per charr among lakes were examined using a series of generalized linear models, with the exception of rare taxa (*Contraecum* sp., *Philonema oncorhynchi*, *Proteocephalus* sp., *Schistocephalus solidus*, *Tetraonchus* sp.), which were excluded from further analysis. Models were fitted with a quasi-Poisson distribution and log-link

function to account for over-dispersion, with the exception of *D. sagittata*, which was fitted with a Poisson distribution and log-link function. To account for the potential bias caused by variation in host age, we included fish length (centred on the mean and scaled by one standard deviation) as a continuous fixed factor in all general and generalized linear models. Contrast analyses were constructed for each model by varying the base lake (intercept) to assess differences between lake pairs. Only significant contrasts are presented in the results.

Results

Component community

Fifteen parasite taxa (4 allogenic AL, 11 autogenic AU) were identified from Arctic charr populations in the Fusta catchment, with

only small differences in taxa richness (11–14 taxa) and community composition observed between lakes (LV–ØV $S_j = 0.29$, LV–FV $S_j = 0.29$, ØV–FV $S_j = 0.33$; table 2). However, most parasites (12 taxa) were generalist taxa also known to infect brown trout, with only three Arctic charr-specialist species present (*Eubothrium salvelini*, *Salmincola edwardsii*, *P. oncorhynchi*). All four allogenic parasites were present in all lakes: metacercarial eye flukes of the trematodes *Diplostomum* sp. and *Tylodelphys* sp. and the larval cestodes *Diphyllobothrium dendriticum* and *D. ditremum*; whereas minor inter-lake differences in the composition and number of autogenic taxa reflected variation in the presence of monogenean (*Discocotyle sagittata*, *Tetraonchus* sp.) and nematode taxa (*Contraecaecum* sp., *P. oncorhynchi*, *Pseudocapillaria* sp.; $S = 7$ LV, 10 ØV, 8 FV; table 2). *Schistocephalus solidus*, an allogenic parasite acquired from consuming infected stickleback (second intermediate host), was noted in the stomach contents of charr at low prevalence and abundance throughout the catchment (table 2). In all lakes, trematodes *Diplostomum* sp. and *Phyllodistomum umblae* were the most common allogenic and autogenic taxa, representing 49–79% and 80–97% of individuals at each lake, respectively.

Infracommunities

Fustvatnet charr (lower catchment) harboured the highest number of parasite taxa and total infracommunity abundance, in addition to higher abundances of allogenic parasites than other lakes (tables 3 and S1). In terms of autogenic parasites, charr from both Fustvatnet and Ømmervatnet harboured more individual parasites than the upper catchment lake, Luktvatnet (tables 3 and S1). Taxa evenness (Berger–Parker), but not diversity (Margalef's), differed between all lakes ($LMM_{Lake}: \chi^2 = 75.3, P < 0.005$; Tukey HSD: all $P < 0.05$; ØV > FV > LV), with *P. umblae* and *Diplostomum* sp. dominating the infracommunities of Ømmervatnet and Fustvatnet, respectively (table 3, fig. 2).

Both autogenic and allogenic parasites showed taxon-specific prevalence patterns: increasing (e.g. AU - *D. sagittata*, AL - *Tylodelphys* sp.), decreasing (e.g. AU - *Crepidostomum* sp., AL - *D. dendriticum*) or remaining unchanged along the catchment gradient (e.g. AU - *S. edwardsii*, AL - *Diplostomum* sp.; table 2). However, for most parasites (7/9 taxa), abundance increased from the upper to lower catchment and showed greatest differences between Luktvatnet and Fustvatnet (fig. 2, table S2). For example, the allogenic trematode eye fluke *Tylodelphys* sp. demonstrated a 10-fold increase in abundance between Luktvatnet and Fustvatnet (fig. 2). Autogenic *Crepidostomum* sp. and allogenic *D. ditremum* were the two exceptions to the general trend, occurring in highest abundance in the upper catchment lake, Luktvatnet (table S2).

Discussion

Catchment-wide parasite abundance and distribution patterns in this lentic-dominated system were in accordance with those reported for lotic systems. We found good support for the prediction of increasing parasite abundance in a downstream direction at both the infracommunity and taxa levels. We also found strong support for the hypothesis that the mobility of the most mobile host determines taxon-specific parasite distribution patterns, with all four allogenic taxa (utilizing piscivorous birds as final hosts) present throughout the entire catchment, whereas their autogenic counterparts (charr as final hosts) demonstrated restricted distributions.

Catchment-scale parasite abundance patterns driven by longitudinal or local factors have been identified to some extent in lotic systems (Blasco-Costa *et al.*, 2013; Salgado-Maldonado *et al.*, 2014), with recent work by Blanaar *et al.* (2016) suggesting that localized processes (e.g. habitat quality, land use) may play even greater roles in structuring fish–parasite communities than large-scale (e.g. distance decay; Poulin, 2003) or longitudinal influences (i.e. the river continuum concept; Vannote *et al.*, 1980). Here too in the lentic-dominated Fusta catchment, abundance patterns may be driven by forces of unidirectional flow transporting infected hosts and/or free-living parasitic stages, and also by the localized increases in agricultural land use (2–15%; NVE, 2015) from the upper to lower catchment sufficient to create a gradient of increasing lake productivity. This coupled with existing climatic gradients enabling lakes in the lower catchment to attain earlier and longer ice-free periods, in addition to reaching higher water temperatures, has the potential to generate localized differences in the abundance of both parasites and their hosts (Hakalahti *et al.*, 2006). Increasing water temperature, for example, may enhance trematode populations directly by enhancing egg development and cercariae release from snail intermediate hosts, in addition to increasing the reproduction rate of uninfected snails (Paull and Johnson, 2011).

It is important to note, however, that taxon-specific variation in parasite abundance may occur at a range of spatial scales, even for parasites sharing the same hosts in their life cycles. At large spatial scales (i.e. latitudes, between islands), parasite abundance may be non-deterministic (e.g. Blasco-Costa *et al.*, 2015), and even at mid-to-large spatial scales (i.e. regional, inter-catchment), where heterogeneity is lower, spatial covariation in abundance has been detected (e.g. Lagrue and Poulin, 2015). In particular, Lagrue and Poulin (2015) demonstrated that although parasite taxa that share all host life stages show greatest similarity in spatial abundance, parasites sharing two out of three host life stages do not necessarily show spatial similarity. Our observations in the Fusta catchment support this theory, with high similarity in *Diplostomum* sp. and *Tylodelphys* sp. spatial abundance trends (gastropod – fish – bird) in comparison to *Crepidostomum* sp. (gastropod or bivalve – arthropod – fish) and *D. ditremum* (copepod – fish – bird) for example. Such spatial variations in parasite abundance are likely to be further promoted by differences in local food webs (Marcogliese *et al.*, 2006), with Bérubé and Curtis (1986) demonstrating how inter-lake differences in benthic invertebrate availability influenced *D. ditremum* burdens in Arctic charr. Although invertebrate communities were not assessed among our study lakes, the majority of charr parasites were trophically transmitted via the consumption of copepods or macroinvertebrates, thus the longitudinal gradient of decreasing *D. ditremum* abundance probably reflects a decreasing proportion of copepods (*D. ditremum* first intermediate host) both in the invertebrate community and charr diet.

In contrast to parasite abundance patterns, clear downstream gradients of parasite community diversity were not observed in the Fusta catchment. Component community taxa richness showed little difference between lakes, probably because of the tendency for the substitution rather than accumulation of parasite taxa along the catchment (e.g. cestode *Proteocephalus* sp. – LV only, monogenean *Discocotyle sagittata* – ØV & FV only), and to a lesser extent, the presence of widespread allogenic taxa with distributions independent of downstream water movement. Although infracommunity taxon richness suggested greater taxa richness may occur in the lower catchment, this was not

Table 2. Life cycle, prevalence (%) and abundance (\pm SE) of Arctic charr parasites (AU, autogenic; AL, allogenic) in lakes of the Fusta catchment, Nordland, Norway.

	Taxa	Life cycle	1st intermediate host	2nd intermediate host	Final host	Luktvatnet	Ømmervatnet	Fustvatnet	Contrasts ^{a,*}	
Monogenea	<i>Discocotyle sagittata</i>	AU	Direct	None	None	Fish	0	18.2 0.17 \pm 0.01	47.8 1.13 \pm 0.3	FV > ØV
	<i>Tetraonchus</i> sp.	AU	Direct	None	None	Fish	0	4.5 0.04 \pm 0.04	0	–
Trematoda	<i>Crepidostomum</i> sp.	AU	Indirect	Gastropod or bivalve	Arthropod	Fish	83.3 9.2 \pm 2.3	27.3 1.5 \pm 0.8	13.0 1.04 \pm 0.6	LV > (FV = ØV)
	<i>Diplostomum</i> sp.	AL	Indirect	Gastropod	Fish	Bird	100 42.0 \pm 4.5	100 22.3 \pm 4.4	100 188.6 \pm 28.2	FV > (ØV = LV)
	<i>Phyllodistomum umblae</i>	AU	Indirect	Gastropod	Arthropod	Fish	100 62.0 \pm 7.0	95.5 159.3 \pm 24.2	73.9 113.6 \pm 33.2	ØV > FV > LV
	<i>Tylodelphys</i> sp.	AL	Indirect	Gastropod	Fish	Bird	41.7 1.3 \pm 0.5	77.3 4.6 \pm 1.0	100 36.2 \pm 6.4	FV > (ØV = LV)
Cestoda	<i>Diphyllobothrium dendriticum</i>	AL	Indirect	Copepod	Fish	Birds, mammals	75 2.0 \pm 0.4	40.9 3.7 \pm 2.9	6 3.9 \pm 1.5	FV > ØV
	<i>Diphyllobothrium ditremum</i>	AL	Indirect	Copepod	Fish	Birds	100 41.6 \pm 6.0	81.8 14.7 \pm 11.4	91.3 12.9 \pm 2.8	LV > ØV > FV
	<i>Eubothrium salvelini</i> #	AU	Indirect	Copepod	None	Fish	16.7 0.4 \pm 0.2	54.5 1.3 \pm 0.5	69.6 1.9 \pm 0.5	NS
	<i>Proteocephalus</i> sp.	AU	Indirect	Copepod	None	Fish	4.2 0.04 \pm 0.04	0	0	–
	<i>Schistocephalus solidus</i>	AL	Indirect	Copepod	Fish	Birds	4.2 0.2 \pm 0.2	4.5 0.04 \pm 0.04	4.3 0.1 \pm 0.1	–
Nematoda	<i>Pseudocapillaria</i> sp.	AU	Indirect	Unknown	Oligochaete	Fish	0	18.2 1.9 \pm 1.4	87.0 24.0 \pm 8.7	FV > ØV
	<i>Contraecum</i> sp.	AU	Indirect	Copepod	Unknown	Fish	4.2 0.04 \pm 0.04	13.6 0.3 \pm 0.2	17.4 0.1 \pm 0.1	–
	<i>Philonema oncorhynchi</i> #	AU	Indirect	Copepod	None	Fish	0	4.5 0.04 \pm 0.04	39.1 0.5 \pm 0.2	–
Copepoda	<i>Salmincola edwardsii</i> #	AU	Direct	None	None	Fish	20.8 0.2 \pm 0.1	13.6 0.1 \pm 0.1	21.7 0.5 \pm 0.2	–
	Taxa richness S						11	14	13	–

^a Summary of inter-lake contrast analyses; see supplementary table S2 for details* $P < 0.05$, NS – not significant

Table 3. Inter-lake differences in parasite infracommunity diversity characteristics (mean \pm standard error) from Arctic charr of the Fusta catchment, Nordland, Norway.

	Luktvatnet (LV)	Ømmervatnet (ØV)	Fustvatnet (FV)	Contrast ^{a, *}
Total abundance, <i>N</i>	154.1 \pm 11.6	217.5 \pm 23.4	403.4 \pm 42.0	Lakes: FV > (ØV > LV), Length: NS, Lake \times Length: NS
Autogenic	72.0 \pm 7.5	174.2 \pm 23.3	166.8 \pm 31.5	Lakes: (ØV = FV) > LV, Length: NS, Lake \times Length: NS
Allogenic	83.9 \pm 8.6	47.1 \pm 17.1	239.8 \pm 32.6	Lakes: FV > (LV > ØV), Length: NS, Lake \times Length: NS
No. of taxa, <i>S</i>	4.8 \pm 0.2	5.1 \pm 0.3	6.7 \pm 0.3	Lakes: FV > (LV = ØV), Length: NS, Lake \times Length: NS
Taxon diversity, <i>D_{Mg}</i>	1.0 \pm 0.0	0.9 \pm 0.1	1.04 \pm 0.1	Lakes: NS, Length: NS, Lake \times Length: NS
Taxon evenness, <i>d</i>	0.5 \pm 0.0	0.8 \pm 0.0	0.6 \pm 0.0	Lakes: (ØV > FV) > LV, Length: NS, Lake \times Length: NS

^a Summary of inter-lake contrast analyses; see supplementary table S1 for details

**P* < 0.05, NS – not significant

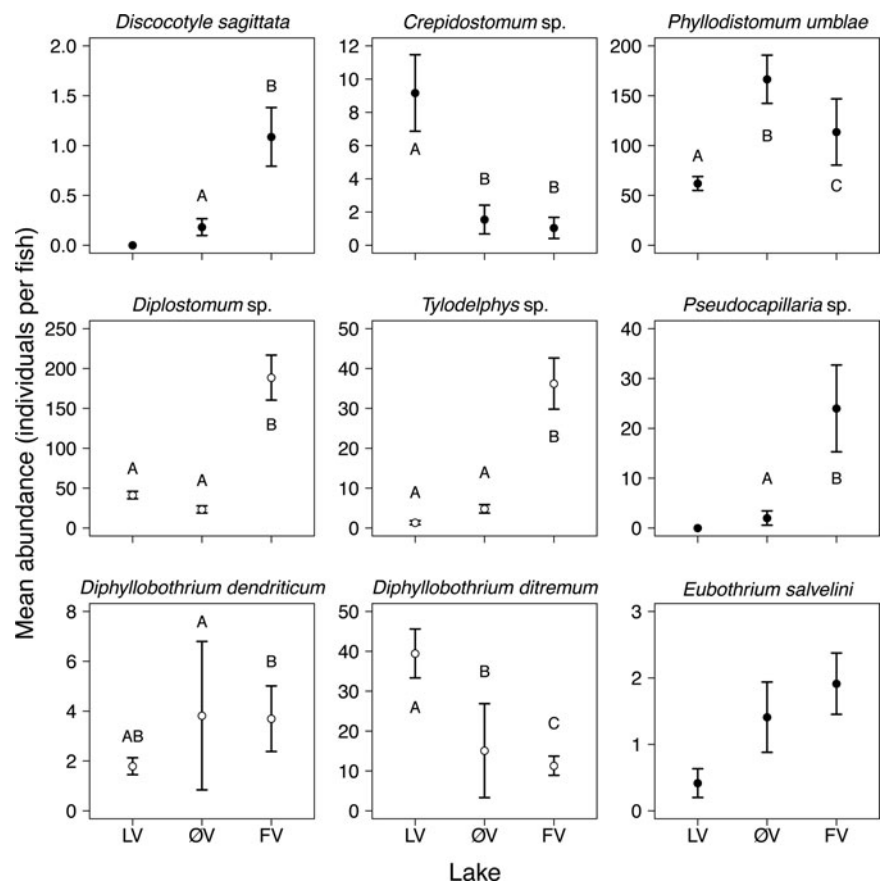


Fig. 2. Parasite abundance in lakes Luktvatnet (LV), Ømmervatnet (ØV) and Fustvatnet (FV), Fusta catchment, Nordland County, Norway. Open circles indicate allogenic taxa, closed circles indicate autogenic taxa, and error bars indicate standard error. Significant differences between lakes are indicated by capital letters (*P* < 0.05; supplementary table S2).

supported by taxa diversity measures when both the individual and taxa abundance were accounted for. Although differences in lake size have the potential to influence parasite species richness (Kennedy, 1978), it is likely that the similarity in depth (62–65 m) among the large lakes in the Fusta catchment (3.8–10.6 km²) minimizes this effect (Marcogliese and Cone, 1991).

The absence of parasite diversity gradients may also be attributed to the majority of autogenic taxa being generalist parasites known to infect brown trout; the migratory (Præbel and Knudsen, 2012) and numerically dominant salmonid species of the Fusta catchment (charr : trout ratio: LV 1 : 1.1, ØV 1 : 7.3, FV 1 : 3.4; Hanssen, 2013). Although parasite dynamics are strongly linked to the relative abundance of their hosts (Arneberg *et al.*, 1998; Paterson *et al.*,

2013), this abundant salmonid species may not be exclusively responsible for the erosion of the autogenic parasite community structure among lakes. For example, autogenic-generalist taxa (e.g. *Proteocephalus* sp., *Pseudocapillaria* sp.) were more patchily distributed in the catchment than autogenic-specialist taxa of charr (e.g. *Eubothrium salvelini*, *Salmincola edwardsii*). Previous comparisons between sympatric trout and charr parasite communities have also demonstrated that charr are often the dominant host, in terms of parasite prevalence, abundance and species richness (e.g. Knudsen *et al.*, 2008, Kristmundsson and Richter, 2009), as a result of greater exposure to infectious stages through their wider habitat and dietary niches (Eloranta *et al.*, 2013), coupled with greater host-parasite compatibility.

Furthermore, there is little evidence to suggest differences in sample year (2013 vs 2012) nor fish sampling methods (gill netting vs rotenone) between Luktvatnet and the lower lakes were responsible for the observed parasite distribution patterns. Although seasonal variation in fish–parasite communities occurs in Norwegian lakes (e.g. Amundsen *et al.*, 2003), inter-annual variability tends to be low (Paterson, unpublished; Kuhn *et al.*, 2016). Rotenone, on the other hand, is detrimental to fish ectoparasite populations via indirect effects on host mortality (e.g. Fukami *et al.*, 1969), and experimental studies suggest rotenone may have anthelmintic properties towards nematodes (Kotze *et al.*, 2006); however, the direct impacts of rotenone on fish parasites are unknown. Thus, we cannot exclude the possibility of rotenone-induced reductions in ectoparasite abundance in lakes Ømmervatnet and Fustvatnet, although influences on the parasitic copepod *S. edwardsii* are likely to be minimal given its securely imbedded bulla structure. Furthermore, we note that both the observed composition and abundance of parasite taxa in charr populations of the Fusta catchment lakes are similar to those of other northern Norwegian lakes (Kennedy, 1977; Amundsen *et al.*, 1997; Knudsen *et al.*, 1997), and thus the effect of the rotenone fish sampling method, if present, should be minimal.

By assessing parasite distribution patterns in the Fusta catchment, our study sheds light on the catchment's potential resilience against environmental disturbances (i.e. the planned salmonid eradication). Although Arctic charr specialist parasites and communities are generally stable through time (Amundsen *et al.*, 1997; Knudsen *et al.*, 2010; Kuhn *et al.*, 2016), they may change as a result of severe anthropogenic disturbances to salmonid populations (Amundsen and Kristoffersen, 1990; Knudsen *et al.*, 2002). Regions that avoid environmental perturbations are considered to be important reservoirs of natural propagules to facilitate the recolonization of biotic assemblages (Tonkin *et al.*, 2014), a feature that may be particularly important for autogenic parasite species with limited inter-catchment dispersal capabilities. However, our assessment of catchment-wide component communities suggests that lakes Ømmervatnet and Fustvatnet may experience long-term reductions in parasite diversity after the rotenone treatment programme. Allogenic taxa with high colonization abilities (i.e. *Diplostomum* sp., *Tylodelphys* sp., *Diphyllbothrium* spp.) would be expected to re-establish throughout the catchment. In contrast, at least four autogenic taxa (i.e. *D. sagittata*, *Tetraonchus* sp., *Pseudocapillaria* sp., *P. oncorhynchi*) may be at risk of eradication, unless sympatric populations of brown trout or three-spined stickleback in Luktvatnet act as reservoir hosts (e.g. Hartvigsen and Halvorsen, 1993; Braicovich *et al.*, 2016). Temporary impacts on Arctic charr-specialist parasite taxa (i.e. *E. salvelini*, *S. edwardsii*) would also be anticipated, although mitigated by the gradual downstream recolonization to treated lakes.

In summary, our study demonstrates the generality of catchment-wide parasite abundance and distribution patterns irrespective of the dominant habitat type. Furthermore, this study suggests that longitudinal gradients in parasite abundance may still arise in lentic-dominated catchments, despite the reduced role of unidirectional water movement.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0022149X18000482>

Acknowledgements. Fish sampling was carried out by Mosjøen og Omegn Næringssselskap in accordance with Norwegian Veterinary Institute regulations. We thank R. Poulin and two anonymous reviewers for constructive comments on an earlier version of this manuscript.

Financial support. This study was supported by the Norwegian Environment Agency and internal funding from the Norwegian Veterinary Institute. RAP was also supported by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement (no. 663830).

Conflict of interest. None.

Ethical standards. All fish were killed following the strict codes of practice in force in Europe. No approval from Institutional Animal Care and Use Committee (IACUC) or ethics committee was necessary.

References

- Amundsen P-A and Kristoffersen R (1990) Infection of whitefish (*Coregonus lavaretus* L. sl) by *Triaenophorus crassus* Forel (Cestoda: Pseudophyllidea): a case study in parasite control. *Canadian Journal of Zoology* **68**, 1187–1192.
- Amundsen P-A, Kristoffersen R, Knudsen R and Klemetsen A (1997) Infection of *Salmincola edwardsii* (Copepoda: Lernaeopodidae) in an age-structured population of Arctic charr - a long-term study. *Journal of Fish Biology* **51**, 1033–1046.
- Amundsen P-A, Knudsen R, Kuris AM and Kristoffersen R (2003) Seasonal and ontogenetic dynamics in trophic transmission of parasites. *Oikos* **102**, 285–293.
- Arneberg P, Skorping A, Grenfell B and Read AF (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London B: Biological Sciences* **265**, 1283–1289.
- Berger WH and Parker FL (1970) Diversity of planktonic foraminifera in deep-sea sediments. *Science* **168**, 1345–1347.
- Bérubé M and Curtis MA (1986) Transmission of *Diphyllbothrium ditremum* to Arctic char (*Salvelinus alpinus*) in two subarctic Quebec lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1626–1634.
- Blanar C, Hewitt M, McMaster M, Kirk J, Wang Z, Norwood W and Marcogliese D (2016) Parasite community similarity in Athabasca River trout-perch (*Percopsis omiscomaycus*) varies with local-scale land use and sediment hydrocarbons, but not distance or linear gradients. *Parasitology Research* **115**, 3853–3866.
- Blasco-Costa I, Rouco C and Poulin R (2015) Biogeography of parasitism in freshwater fish: spatial patterns in hot spots of infection. *Ecography* **38**, 301–310.
- Blasco-Costa I, Poulin R and Presswell B (2017) Morphological description and molecular analyses of *Tylodelphys* sp. (Trematoda: Diplostomidae) newly recorded from the freshwater fish *Gobiomorphus cotidianus* (common bully) in New Zealand. *Journal of Helminthology* **91**, 332–345.
- Blasco-Costa I, Koehler AV, Martin A and Poulin R (2013) Upstream-downstream gradient in infection levels by fish parasites: a common river pattern? *Parasitology* **140**, 266–274.
- Blasco-Costa I, Faltýnková A, Georgieva S, Skirnisson K, Scholz T and Kostadinova A (2014) Fish pathogens near the Arctic Circle: molecular, morphological and ecological evidence for unexpected diversity of *Diplostomum* (Digenea: Diplostomidae) in Iceland. *International Journal for Parasitology* **44**, 703–715.
- Braicovich PE, Kuhn JA, Amundsen P-A and Marcogliese DJ (2016) Three-spined stickleback *Gasterosteus aculeatus*, as a possible paratenic host for salmonid nematodes in a subarctic lake. *Parasitology Research* **115**, 1335–1338.
- Bush AO, Lafferty KD, Lotz JM and Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Clifford HT and Stephenson W (1975) *An Introduction to Numerical Classification*. New York, NY: Academic Press.
- Eloranta A, Knudsen R and Amundsen P-A (2013) Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology* **58**, 207–221.
- Esch GW, Kennedy CR, Bush AO and Aho JM (1988) Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology* **96**, 519–532.

- Fukami JI, Shishido T, Fukunaga K and Casida JE** (1969) Oxidative metabolism of rotenone in mammals, fish and insects, and its relation to selective toxicity. *Journal of Agricultural Food Chemistry* **17**, 1217–1226.
- Hakalahti T, Karvonen A and Valtonen E** (2006) Climate warming and disease risks in temperate regions—*Argulus coregoni* and *Diplostomum spathaceum* as case studies. *Journal of Helminthology* **80**, 93–98.
- Hanssen ØK** (2013) Kartlegging av fiskebestandene i Fustavassdraget i forkant av rotenonbehandling. 2013–06. 978-82-8312-039-4, Ferskvannsbiolegen, Lødingen. (In Norwegian).
- Hartvigsen R and Halvorsen O** (1993) Common and rare trout parasites in a small landscape system. *Parasitology* **106**, 101–105.
- Heino J, Virkkala R and Toivonen H** (2009) Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* **84**, 39–54.
- Hofmann H, Blasco-Costa I, Knudsen R, Matthaei CD, Valois A and Lange K** (2016) Parasite prevalence in an intermediate snail host is subject to multiple anthropogenic stressors in a New Zealand river system. *Ecological Indicators* **60**, 845–852.
- Jackson DA, Peres-Neto PR and Olden JD** (2001) What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 157–170.
- Kelly DW, Poulin R, Tompkins DM and Townsend CR** (2010) Synergistic effects of glyphosate formulation and parasite infection on fish malformations and survival. *Journal of Applied Ecology* **47**, 498–504.
- Kennedy CR** (1977) Distribution and zoogeographical characteristics of the parasite fauna of char *Salvelinus alpinus* in Arctic Norway, including Spitsbergen and Jan Mayen islands. *Astarte* **10**, 49–55.
- Kennedy CR** (1978) An analysis of the metazoan parasitocoenoses of brown trout *Salmo trutta* from British Lakes. *Journal of Fish Biology* **13**, 255–263.
- Knudsen R, Kristoffersen R and Amundsen PA** (1997) Parasite communities in two sympatric morphs of Arctic charr, *Salvelinus alpinus* (L.), in northern Norway. *Canadian Journal of Zoology* **75**, 2003–2009.
- Knudsen R, Amundsen P-A and Klemetsen A** (2002) Parasite-induced host mortality: indirect evidence from a long-term study. *Environmental Biology of Fishes* **64**, 257–265.
- Knudsen R, Amundsen P-A, Nilsen R, Kristoffersen R and Klemetsen A** (2008) Food borne parasites as indicators of trophic segregation between Arctic charr and brown trout. *Environmental Biology of Fishes* **83**, 107–116.
- Knudsen R, Primicerio R, Amundsen P-A and Klemetsen A** (2010) Temporal stability of individual feeding specialization may promote speciation. *Journal of Animal Ecology* **79**, 161–168.
- Kotze AC, Dobson RJ and Chandler D** (2006) Synergism of rotenone by piperonyl butoxide in *Haemonchus contortus* and *Trichostrongylus colubriformis* in vitro: potential for drug-synergism through inhibition of nematode oxidative detoxification pathways. *Veterinary Parasitology* **136**, 275–282.
- Kristmundsson Á and Richter SH** (2009) Parasites of resident Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*, in two lakes in Iceland. *Icelandic Agricultural Sciences* **22**, 5–18.
- Kuhn JA, Knudsen R, Kristoffersen R, Primicerio R and Amundsen P-A** (2016) Temporal changes and between-host variation in the intestinal parasite community of Arctic charr in a subarctic lake. *Hydrobiologia* **783**, 79–91.
- Lagroe C and Poulin R** (2015) Spatial covariation of local abundance among different parasite species: the effect of shared hosts. *Parasitology Research* **114**, 3637–3643.
- Magurran AE** (2003) *Measuring Biological Diversity*. Oxford: Blackwell Science.
- Marcogliese DJ and Cone DK** (1991) Importance of lake characteristics in structuring parasite communities of salmonids from insular Newfoundland. *Canadian Journal of Zoology* **69**, 2962–2967.
- Marcogliese DJ, Gendron AD, Plante C, Fournier M and Cyr D** (2006) Parasites of spottail shiners (*Notropis hudsonius*) in the St. Lawrence River: effects of municipal effluents and habitat. *Canadian Journal of Zoology* **84**, 1461–1481.
- Morley NJ** (2007) Anthropogenic effects of reservoir construction on the parasite fauna of aquatic wildlife. *EcoHealth* **4**, 374–383.
- NVE (Norges vassdrags- og energidirektorat / The Norwegian Water Resources and Energy Directorate)** (2015) *NVE Atlas 3.0*. Available at www.nve.no/karttjenester/kartverktoy/nve-atlas/
- Oros M and Hanzelová V** (2009) Re-establishment of the fish parasite fauna in the Tisa River system (Slovakia) after a catastrophic pollution event. *Parasitology Research* **104**, 1497–1506.
- Ostfeld RS, Glass GE and Keesing F** (2005) Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* **20**, 328–336.
- Paterson RA, Rauque CA, Fernandez MV, Townsend CR, Poulin R and Tompkins DM** (2013) Native fish avoid parasite spillback from multiple exotic hosts: consequences of host density and parasite competency. *Biological Invasions* **15**, 2205–2218.
- Paull SH and Johnson PT** (2011) High temperature enhances host pathology in a snail-trematode system: possible consequences of climate change for the emergence of disease. *Freshwater Biology* **56**, 767–778.
- Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team** (2017) Package ‘nlme’: linear and nonlinear mixed effects models. R version 3–1. Available at <http://CRAN.R-project.org/package=nlme>.
- 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** (2003) The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *Journal of Biogeography* **30**, 1609–1615.
- Poulin R and Valtonen ET** (2002) The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. *International Journal for Parasitology* **32**, 1235–1243.
- Præbel K and Knudsen R** (2012) Genetiske undersøkelser av ørret (*Salmo trutta*) og røye (*Salvelinus alpinus*) i Fustavassdraget med henblikk på å bevare genetisk diversitet og variasjon etter rotenonbehandling. UiT - The Arctic University of Norway. (In Norwegian).
- R Development Core Team** (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Salgado-Maldonado G, Novelo-turcotte MT, Vazquez G, Caspetamandujano JM, Quiroz-Martinez B and Favila M** (2014) The communities of helminth parasites of *Heterandria bimaculata* (Teleostei: Poeciliidae) from the upper Río La Antigua basin, east-central Mexico show a predictable structure. *Parasitology* **141**, 970–980.
- Sæter L** (1995) Overvåking av ungfisbestand og utbredelsen av lakseparasitten *Gyrodactylus salaris* i Nordland 1990–1994. - Fylkesmannen i Nordland, Miljøvernnavdelingen, Rapport 3–1995: 1–195.
- Siwertsson A, Refsnes B, Frainer A, Amundsen P-A and Knudsen R** (2016) Divergence and parallelism of parasite infections in Arctic charr morphs from deep and shallow lake habitats. *Hydrobiologia* **783**, 131–143.
- Skoglund S, Siwertsson A, Amundsen P-A and Knudsen R** (2015) Morphological divergence between three Arctic charr morphs—the significance of the deepwater environment. *Ecology and Evolution* **5**, 3114–3129.
- Sterud E** (1999) Parasitter hos norske ferskvannsfisk. *Norsk Zoologisk Forening*, Oslo. Rapport 7. (In Norwegian).
- Tonkin JD, Stoll S, Sundermann A and Haase P** (2014) Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology* **59**, 1843–1855.
- Valtonen E, Holmes J and Koskivaara M** (1997) Eutrophication, pollution and fragmentation: effects on parasite communities in roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in four lakes in central Finland. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 572–585.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR and Cushing CE** (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137.
- Woodward G, Perkins DM and Brown LE** (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**, 2093–2106.