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


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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 is 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; autogenic 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,
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 freshwater; 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 6 months (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 infracomunity (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 \( d \)).
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 \( D_{\text{Marg}} \) 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 (Contracaecum sp., Philonema onchorhynchi, 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 taxon richness (11–14 taxa) and community composition observed between lakes (LV–OV Sjack = 0.29, LV–FV Sjack = 0.29, ÖV–FV Sjack = 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 autochthonous taxa reflected variation in the presence of monogenean (Discocotyle sagittata, Tetraonchus sp.) and nema-
tode taxa (Contracaecum sp., P. oncorhynchi, Pseudocapillaria sp.; S = 7 LV, 10 ÖV, 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 umbilae were the most common allogenic and autochthonous 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 autochthonous parasites, charr from both Fustvatnet and Ömmervatnet 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 (LMMLake: χ² = 75.3, P < 0.005; Tukey HSD: all P < 0.05; ÖV > FV > LV), with P. umbilae and Diplostomum sp. dominating the infracommunities of Ömmervatnet 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 gra-
dient (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 longi-
tudinal 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 Blanar 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 catch-
ment 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 (Hakalahliti et al., 2006). Increasing water temperature, for example, may enhance trematode populations directly by enhan-
cing egg development and cercariae release from snail intermedi-
ate 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 abund-
ance 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 (cope-
pod – 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 trop-
ically transmitted via the consumption of copepods or macro-
invertebrates, 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 – ÖV & 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 (± SE) of Arctic charr parasites (AU, autogenic; AL, allogenic) in lakes of the Fusta catchment, Nordland, Norway.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Life cycle</th>
<th>1st intermediate host</th>
<th>2nd intermediate host</th>
<th>Final host</th>
<th>Luktvatnet</th>
<th>Ømmervatnet</th>
<th>Fustvatnet</th>
<th>Contrasts(^a^)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monogenea Discocotyle sagittata</td>
<td>AU</td>
<td>Direct</td>
<td>None</td>
<td>None</td>
<td>0</td>
<td>18.2</td>
<td>47.8</td>
<td>FV &gt; ØV</td>
</tr>
<tr>
<td>Tetraonchus sp.</td>
<td>AU</td>
<td>Direct</td>
<td>None</td>
<td>None</td>
<td>0</td>
<td>4.5</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td>Trematoda Crepidostomum sp.</td>
<td>AU</td>
<td>Indirect</td>
<td>Gastropod or bivalve</td>
<td>Arthropod</td>
<td>83.3</td>
<td>9.2 ± 2.3</td>
<td>13.0</td>
<td>LV &gt; (FV = ØV)</td>
</tr>
<tr>
<td>Diplostomum sp.</td>
<td>AL</td>
<td>Indirect</td>
<td>Gastropod</td>
<td>Fish</td>
<td>100</td>
<td>22.3 ± 4.4</td>
<td>100</td>
<td>FV &gt; (ØV = LV)</td>
</tr>
<tr>
<td>Phylodistomum umbloe</td>
<td>AU</td>
<td>Indirect</td>
<td>Gastropod</td>
<td>Fish</td>
<td>100</td>
<td>95.5</td>
<td>73.9</td>
<td>ØV &gt; FV &gt; LV</td>
</tr>
<tr>
<td>Tylodelphys sp.</td>
<td>AL</td>
<td>Indirect</td>
<td>Gastropod</td>
<td>Fish</td>
<td>41.7</td>
<td>4.6 ± 1.0</td>
<td>100</td>
<td>FV &gt; (ØV = LV)</td>
</tr>
<tr>
<td>Cestoda Diphyllobothrium dendriticum</td>
<td>AL</td>
<td>Indirect</td>
<td>Copepod</td>
<td>Fish</td>
<td>75</td>
<td>40.9</td>
<td>6</td>
<td>FV &gt; ØV</td>
</tr>
<tr>
<td>Diphyllobothrium ditremum</td>
<td>AL</td>
<td>Indirect</td>
<td>Copepod</td>
<td>Fish</td>
<td>100</td>
<td>81.8</td>
<td>91.3</td>
<td>LV &gt; ØV &gt; FV</td>
</tr>
<tr>
<td>Eubothrium salvelini^#</td>
<td>AU</td>
<td>Indirect</td>
<td>Copepod</td>
<td>None</td>
<td>16.7</td>
<td>1.3 ± 0.5</td>
<td>69.6</td>
<td>NS</td>
</tr>
<tr>
<td>Proteocephalus sp.</td>
<td>AU</td>
<td>Indirect</td>
<td>Copepod</td>
<td>None</td>
<td>4.2</td>
<td>0.4 ± 0.04</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td>Schistocephalus solidus</td>
<td>AL</td>
<td>Indirect</td>
<td>Copepod</td>
<td>Fish</td>
<td>4.2</td>
<td>4.5</td>
<td>4.3</td>
<td>–</td>
</tr>
<tr>
<td>Nematoda Pseudocapillaria sp.</td>
<td>AU</td>
<td>Indirect</td>
<td>Unknown</td>
<td>Oligochaete</td>
<td>0</td>
<td>18.2</td>
<td>87.0</td>
<td>FV &gt; ØV</td>
</tr>
<tr>
<td>Contracaecum sp.</td>
<td>AU</td>
<td>Indirect</td>
<td>Copepod</td>
<td>Unknown</td>
<td>4.2</td>
<td>13.6</td>
<td>17.4</td>
<td>–</td>
</tr>
<tr>
<td>Philonema oncorhynchi^#</td>
<td>AU</td>
<td>Indirect</td>
<td>Copepod</td>
<td>None</td>
<td>0</td>
<td>4.5</td>
<td>39.1</td>
<td>–</td>
</tr>
<tr>
<td>Copepoda Salmincola edwardsii^#</td>
<td>AU</td>
<td>Direct</td>
<td>None</td>
<td>None</td>
<td>20.8</td>
<td>13.6</td>
<td>21.7</td>
<td>–</td>
</tr>
<tr>
<td>Taxa richness S</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11</td>
<td>14</td>
<td>13</td>
<td>–</td>
</tr>
</tbody>
</table>

* Summary of inter-lake contrast analyses; see supplementary table S2 for details

^\(^*\)P < 0.05, NS – not significant
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., *Psuedocapillaria* sp.) were more patchily distributed in the catchment than autogenic-specialist taxa of charr (e.g. *Eubothrium salvelini*, *Salmincola edwardsii*).

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

<table>
<thead>
<tr>
<th></th>
<th>Luktvatnet (LV)</th>
<th>Ømmervatnet (ØV)</th>
<th>Fustvatnet (FV)</th>
<th>Contrast† ‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total abundance, $N$</td>
<td>154.1 ± 11.6</td>
<td>217.5 ± 23.4</td>
<td>403.4 ± 42.0</td>
<td>Lakes: FV &gt; (ØV &gt; LV), Length: NS, Lake × Length: NS</td>
</tr>
<tr>
<td>Autogenic</td>
<td>72.0 ± 7.5</td>
<td>174.2 ± 23.3</td>
<td>166.8 ± 31.5</td>
<td>Lakes: (ØV = FV) &gt; LV, Length: NS, Lake × Length: NS</td>
</tr>
<tr>
<td>No. of taxa, $S$</td>
<td>4.8 ± 0.2</td>
<td>5.1 ± 0.3</td>
<td>6.7 ± 0.3</td>
<td>Lakes: FV &gt; (LV &gt; ØV), Length: NS, Lake × Length: NS</td>
</tr>
<tr>
<td>Taxon diversity, $D_{MG}$</td>
<td>1.0 ± 0.0</td>
<td>0.9 ± 0.1</td>
<td>1.04 ± 0.1</td>
<td>Lakes: NS, Length: NS, Lake × Length: NS</td>
</tr>
<tr>
<td>Taxon evenness, $d$</td>
<td>0.5 ± 0.0</td>
<td>0.8 ± 0.0</td>
<td>0.6 ± 0.0</td>
<td>Lakes: (ØV &gt; FV) &gt; LV, Length: NS, Lake × Length: NS</td>
</tr>
</tbody>
</table>

† 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).
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 ectoparasites 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 Ommervatnet and Fustvatnet, although influences on the parasitic copepod S. edwardsii are likely to be minimal given its securely imbedded bula 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 Ommervatnet and Fustvatnet may experience long-term reductions in parasite diversity after the rotenone treatment program. Allogenic taxa with high colonization abilities (i.e. Diplodistomum sp., Tylodelphys sp., Diplodilbothrium 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 down-stream 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

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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.

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