



Exploring trophic niches and parasite communities of sympatric Arctic charr and brown trout populations of southern Norway

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Abstract Catchment-scale variation between lake habitats has the potential to simultaneously influence the trophic niche and parasite community of fish hosts. In this study, we investigated the trophic niche and parasite community of sympatric Arctic charr and brown trout populations from two inter-connected southern Norwegian lakes at different altitudes. Arctic charr and brown trout occupied profundal and littoral habitats in each lake, respectively, whereas brown trout replaced Arctic charr in pelagic habitats of the

lower altitude lake. Distinct between-lake differences in diet and parasite community composition were noted for brown trout; however, both fish species showed highly overlapping trophically transmitted parasite communities regardless of the habitats each species used. Our results suggest that environmental differences over relatively limited geographical distances have the potential to influence fish habitat use and parasite community structure.

Keywords *Salvelinus alpinus* · *Salmo trutta* · Species richness · Diet

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Introduction

Environment-induced alterations to distribution patterns of co-evolved species have the potential to uncouple trophic interactions essential for maintaining freshwater ecosystem structure and function (Winder & Schindler, 2004). Whilst temperature-related shifts in freshwater fish distribution patterns associated with range expansion or constrictions of cold and cool-water species are recognised (Comte et al., 2013), interactions involving parasites are frequently overlooked, despite the significant role parasites play in aquatic food web complexity and topology (Amundsen et al., 2009). Moreover, environmental gradients capable of uncoupling trophic interactions may not be

restricted to latitudinal scales, with local environmental variation at the catchment scale (e.g. 0.65°C temperature decrease per 100 m altitude increase; Oskar Landgren, Norwegian Meteorological Institute, *pers. comm.*) also having the potential to simultaneously influence both the trophic niche and parasite assemblages of fish communities.

Sympatric Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) populations in Norwegian lakes provide ideal study systems to assess local variability in trophic niche and parasite assemblages. Arctic charr have high phenotypic plasticity, capable of exploiting foraging resources from littoral, pelagic and profundal lake habitats (Klemetsen et al., 2003a). However, when in sympatry with brown trout, interspecific resource competition often results in the exclusion of Arctic charr from littoral habitats (e.g. Nilsson, 1963; Eloranta et al., 2013). Increasing water temperature and reduced dissolved oxygen in lake surface waters associated with climate change and anthropogenic stressors may further promote the constriction of exploitable habitat for the cold-water specialist Arctic charr (e.g. Elliott & Elliott, 2010; Jeppesen et al., 2012). In contrast, the higher temperature tolerance of brown trout (Elliott & Elliott, 2010) may to some extent facilitate the range expansion of this cool-water fish species into lake habitat niches made vacant by rising water temperatures.

Within-lake habitat shifts are likely to simultaneously result in parasite burden shifts, through both changes in diet (trophically transmitted parasites) and contact with free-living parasitic stages (e.g. trematode cercariae released from littoral dwelling snails). Examples from sympatric brown trout and Arctic charr populations show that brown trout parasite assemblages are dominated by taxa which utilise insect larvae and benthic crustacean prey from littoral habitats as intermediate hosts (e.g. *Crepidostomum* spp., Knudsen et al., 2008; Kristmundsson & Richter, 2009). In contrast, pelagic Arctic charr are infected with parasite taxa associated with zooplankton prey (e.g. cestodes *Dibothriocephalus* spp., *Proteocephalus* sp. and *Eubothrium salvelini* (Schränk)), whereas parasites of profundal Arctic charr tend to be those associated with soft bottom benthic invertebrate prey, which are considered to be parasite species-poor hosts (Skoglund et al., 2013; Knudsen et al., 2016; Siwertsson et al., 2016). Brown trout may also acquire cestode infections via piscivory (e.g.

Dibothriocephalus spp. and *Eubothrium crassum* (Bloch); Curtis, 1984; Williams & Jones, 1994). Such trophically transmitted parasites are acquired throughout the active foraging period for these salmonid hosts (Knudsen, 1995), and whilst diet analysis provides only a “snapshot” of the trophic niche, several studies have demonstrated that parasite community assemblages reveal the trophic niche of their hosts akin to other time-integrated measures (e.g. stable isotopes; Knudsen et al., 2014).

Currently, there is a plethora of studies from northern Norwegian lakes investigating parasite community structure across fish assemblages (e.g. Kennedy, 1977; Knudsen, 1995; Knudsen et al., 2008; Siwertsson et al., 2016; Kuhn et al., 2016b; Mocchetti et al., this volume). However, in southern Norway, where anthropogenic impacts to freshwater habitats may be most pronounced (e.g. increasing water temperature, invasive species introduction, agricultural runoff; Rask et al., 2000), research to date has focussed on single parasite–host/s associations (e.g. Vik, 1963; Halvorsen, 1970). In this study, we investigated the relationship between resource use and parasite assemblages of sympatric of Arctic charr and brown trout populations in two inter-connected lakes in southern Norway. We hypothesise that in the absence of local environmental differences, we would observe no difference in habitat use, diet or parasite community of each fish species between lakes. Specifically, we would predict to find Arctic charr occupying pelagic and profundal lake habitats and feeding predominantly on zooplankton prey, with brown trout occupying littoral habitats and feeding on benthos prey. We also hypothesise that parasite diversity and abundance would be higher in Arctic charr than sympatric brown trout (Knudsen et al., 2008), and that parasite abundance would be greater in the lower altitude lake (Paterson et al., 2018).

Materials and methods

Study lakes

Sympatric Arctic charr and brown trout populations were sampled in August 2017 from two lakes of the Skjenaldelva catchment, southern Trøndelag, Norway; Våvatnet (63°19'N, 09°32'E; 425 ha; max. depth 70 m, 300 m.a.s.l.) and Gangåsvatnet (63°16'N,

09°38'E; 549 ha, max. depth 33 m, 153 m.a.s.l.). The lakes are connected via rivers Sagelva and Songa, and lake Songsjøen. There is a theoretical possibility for juvenile fish to migrate downstream, but not upstream due to the presence of a 6.7 m high hydropower dam at the outlet of Våvatnet. Both lakes are dimictic, oligotrophic and ice-free from May to December. Surrounding land use consists of pine and birch forest with some bogs. Small areas of modified agricultural land are present in the Gangåsvatnet catchment only. Water–temperature profiles were measured at 1 m intervals at each lake during fish sampling using a handheld YSI Professional Plus meter (YSI Inc., Yellow Springs, OH, U.S.A.). Late August water temperatures were higher in Gangåsvatnet, with 14.5°C from 0 to 9 m depth, then gradually decreasing from 11.8°C at 10 m to 7.5°C at 20 m. In Våvatnet, surface waters to 11 m deep were 13.0°C, decreasing to 11.9°C at 12 m and 7.0°C at 20 m. Standardised Secchi depth was 4.5 m and 6 m in Gangåsvatnet and Våvatnet, respectively. The Våvatnet fish community consists of Arctic charr and brown trout populations only, whereas three-spined stickleback (*Gasterosteus aculeatus* L.) are also present in Gangåsvatnet. Further details about the fish populations in Våvatnet are provided by Langeland et al. (1991) and L'Abée-Lund et al. (1993).

Sample collection

Arctic charr and brown trout were sampled in August 2017 using a series of multi-mesh panel gillnets (mesh size: 10–55 mm, knot-to-knot, in 5-m panel) set overnight for two nights per lake in the littoral (0–15 m depths), profundal (> 20 m) zones (benthic nets, 1.5 m high, 40 m long), and in the pelagic zone (floating nets, 6 m high, 40 m long). In each lake, nine gillnets were used in the littoral zone, eight in the profundal zone and four in the pelagic zone (0–6 m depth). In Gangåsvatnet, two additional floating nets were also set in the 6–12 m depth zone. Gill-netted fish were euthanized following the strict codes of practice in force in Europe, and approval from Institutional Animal Care and Use Committee (IACUC) was not necessary. The length (fork length, mm), weight (g) and morphotype (littoral-spawning omnivore-, profundal-spawning piscivore- or profundal-spawning benthivore-morphs of Arctic charr only; Skoglund et al., 2015) were obtained from each fish at time of

capture. To characterise the parasite communities, we primarily selected fish with fork length of 200–250 mm to minimise the potential effects of host age on parasite acquisition (Poulin, 2000; Table 1). Fish age (years) was determined from surface readings of ethanol preserved whole otoliths (Kristoffersen & Klemetsen, 1991). In brief, the number of annuli were counted from the lateral otolith surface observed in a glycerol-filled black well plate under 6–50 × magnification by two experienced otolith readers. The body condition of each fish was assessed using Fulton's condition factor (Ricker, 1975):

$$K = \frac{100 \times \text{weight (g)}}{\text{length (cm)}^3}$$

Parasite and diet examinations

External surfaces (e.g. fins, gill opercula) were macroscopically examined for the presence of ectoparasites (e.g. *Argulus* sp.). Eyes, alimentary tract, swim bladder and kidney were systematically screened using a dissection microscope for endoparasites, with all recovered parasites fixed in 96% ethanol after identification. Parasite identification was based on previously described species in Norwegian Arctic charr and brown trout populations (see Sterud, 1999; Moravec, 2004), with parasite infection expressed as prevalence (percentage of fish infected with particular parasite taxon) and abundance (number of individuals of a particular parasite taxon per host; sensu Bush et al., 1997). Larval *Dibothriocephalus dendriticus* (Nitzsch) and *D. ditremus* (Creplin) (formerly *Diphyllobothrium dendriticum* and *D. ditremum*; Waeschenbach et al., 2017) were identified to genus level only. Trematode metacercariae (*Diplostomum* spp., *Tylodelphys* sp., *Apatemon* sp.) present in the eye of each fish were estimated from the left eye only. Comparisons among Arctic charr and brown trout populations from multiple lakes in Norway where both eyes were examined indicate trematode metacercariae do not display a left–right infection bias in these host species (Paterson & Blasco-Costa, unpublished), and thus, dissections of a single eye per fish provides a robust assessment of trematode metacercariae prevalence and abundance. In cases where metacercariae were absent in the left eye ($n = 3$, Våvatnet brown trout), the right eye was

Table 1 Study lake and fish population (Arctic charr *Salvelinus alpinus* (AC) and brown trout *Salmo trutta* (BT)) characteristics

| Lake | Altitude (masl) | Area (ha) | Depth (m) | Location | Habitat | Species | Number sampled | Fork length (mm) | | Total weight (g) | | Condition factor (K) | | Age (years) | |
|--------------|-----------------|-----------|-----------|---------------------|-----------|---------|----------------|------------------|-------|------------------|--------|----------------------|--------|-------------|-------|
| | | | | | | | | Mean | ± SE | Mean | ± SE | Mean | ± SE | Mean | ± SE |
| Gangåsvatnet | 153 | 549 | 33 | 63°16'N, 09°38'E | Littoral | BT | 15 | 240.5 | ± 8.3 | 155.0 | ± 14.0 | 1.07 | ± 0.02 | 3.8 | ± 0.1 |
| | | | | | Pelagic | BT | 13 | 234.1 | ± 6.6 | 138.5 | ± 11.8 | 1.05 | ± 0.01 | 3.7 | ± 0.1 |
| | | | | | Profundal | AC | 35 | 228.7 | ± 3.2 | 133.3 | ± 4.5 | 1.10 | ± 0.01 | 5.6 | ± 0.2 |
| Våvatnet | 300 | 425 | 70 | 63°19'N, 09°32'E | Littoral | BT | 26 | 225.9 | ± 6.0 | 119.3 | ± 6.9 | 1.04 | ± 0.03 | 3.9 | ± 0.2 |
| | | | | | Pelagic | AC | 6 | 214.0 | ± 6.7 | 116.9 | ± 11.8 | 1.17 | ± 0.02 | 5.0 | ± 0.4 |
| | | | | | Profundal | AC | 17 | 223.4 | ± 5.3 | 125.2 | ± 9.0 | 1.10 | ± 0.04 | 5.0 | ± 0.3 |

also examined to confirm the infection status. All dietary contents and parasites associated with the stomach were also fixed in 96% ethanol before identification to the lowest feasible taxonomic level ($n = 22$ prey taxa; see Eloranta et al., 2013 for more details). Prey were placed into four categories (i—adult insects, ii—benthos [e.g. *Eurycercus* sp., chironomid and Ephemeroptera larvae], iii—zooplankton [e.g. *Daphnia* sp., *Polyphemus* sp., *Bosmina* sp.], iv—fish), with their relative contribution to the diet expressed as a percentage of stomach fullness (Amundsen et al., 1996).

Statistical analyses

All statistical analyses were conducted in R version 3.4.2 (R Core Development Team, 2017). Normality and variance assumptions required for parametric tests were confirmed prior to analyses. In cases where normality and variance assumptions could not be met, we fitted appropriate model distributions. Analysis of variance was used to explore differences in body condition between fish species and lakes, whereas differences in fish age were assessed using a generalised linear model fitted with a Poisson distribution to account for over-dispersion. Differences in parasite taxon richness (number of parasite taxa per fish) and abundance (number of individual parasites per fish) between fish species and lakes were tested using separate general linear models and generalised linear models (quasipoisson distribution), respectively. Fish age was included as a variable in both latter models to account for the accumulation of parasites over time (Poulin, 2000). Only significant contrasts are presented in the results.

Canonical Correlation Analysis (vegan::CCorA version 2.4-5; Oksanen et al., 2017) was used to explore correlations between individual diet and parasite community composition between fish species, lakes and habitats. Abundance of trophically transmitted parasites and percentage prey volume for each individual fish were log- and chord-transformed, respectively, prior to analysis.

Results

Fish community

A total of 423 fish were sampled from lakes Gangåsvatnet and Våvatnet, with Arctic charr and brown trout displaying contrasting habitat use between lakes. In Våvatnet, Arctic charr were the dominant species in the pelagic (87.5%, $n = 64$; 0–6 m) and profundal (100%, $n = 35$) habitats, with brown trout dominating the littoral habitats (97.5%, $n = 120$). In contrast, brown trout dominated both littoral (98.4%, $n = 125$) and pelagic (96.8%, $n = 31$; 0–12 m) habitats in Gangåsvatnet, with Arctic charr dominating the profundal habitats (95.8%, $n = 48$). Sampled Arctic charr for parasite studies ($n = 58$, Table 1) were on average one to two years older than brown trout ($n = 54$) from the same lake ($z = 23.99$, $P < 0.001$) and in better body condition ($F_{1,110} = 9.57$, $P = 0.003$; Table 1). Morphology characteristics indicated all Arctic charr belonged to the littoral-spawning omnivore morph.

Diet

Zooplankton, specifically *Daphnia* sp. and *Polyphe-mus* sp., was the dominant prey group for Arctic charr populations in both lakes regardless of habitat use (84.7–96.8% stomach fullness; Table S1). Benthos (e.g. *Eurycercus* sp., chironomid larvae) abundance was higher in Arctic charr from Våvatnet than in Gangåsvatnet. Zooplankton was also the dominant prey for brown trout captured in littoral and pelagic habitats of Gangåsvatnet, though benthos and adult insects were major components of the diet of brown trout in the littoral habitats of both lakes. Fish were largely absent from the stomach contents of Arctic charr and brown trout from the study lakes, with the exception of Arctic charr from the profundal habitat of Gangåsvatnet, where 3–5 three-spined sticklebacks were present in the stomach contents of three charr (80–100% fullness).

Parasite community composition

Ten parasite taxa were identified from Arctic charr and seven taxa from brown trout in the study lakes, of which six and four taxa were trophically transmitted to their respective fish host (Table 2). With the exception

of the trematode *Diplostomum* sp., which are transmitted to fish via free-living larvae, the trophically transmitted adult trematode *Phyllodistomum umblae* (Fabricius) and larval cestode *Dibothriocephalus* spp. were the most common parasite taxa in both fish hosts. Adult cestodes *E. salvelini* and *Proteocephalus* sp. were also frequently observed in Arctic charr, and *E. crassum* in brown trout. Parasite taxon richness was the highest in Arctic charr, and did not differ overall between lakes, whereas brown trout acquired fewer parasites in Våvatnet than Gangåsvatnet (Fig. 1, Table 2; $GLM_{LAKE:FISH}$: $F_{1,106} = 7.612$, $P = 0.007$, Tukey HSD post hoc $P < 0.001$). Total parasite abundance was greater in Arctic charr than brown trout (Fig. 1; GLM_{FISH} : $F_{1,103} = 67.34$, $P < 0.001$), with no observed interaction between fish species and lakes. Neither parasite taxon richness nor abundance was influenced by host age.

The diet of each individual fish significantly described the community of trophically transmitted parasites (Canonical Correlation adjusted $R^2 = 0.27$, $P < 0.001$), and revealed distinct groups of overlapping resource use and parasite acquisition (Fig. 2). Canonical correlation axis 1 strongly opposed individual charr and trout that consumed zooplankton from those individuals consuming benthos and adult insects, resulting in both the separation of Våvatnet brown trout from Arctic charr, and the high overlap in resource use of Arctic charr populations regardless of lake or habitat. Canonical correlation axis 1 also opposed the cestode species *Proteocephalus* sp., *Dibothriocephalus* spp. and *E. salvelini* from trematode *Crepidostomum* spp., mirroring the separation in the fish populations observed from the diet composition. Canonical correlation axis 2 opposed *E. crassum* from all other parasite taxa, revealing the overlapping niche of Gangåsvatnet brown trout from both littoral and pelagic habitats which is distinct from all other fish populations.

Discussion

In general, Arctic charr and brown trout demonstrated distinct trophic niches and parasite communities in the two inter-connected study lakes. Arctic charr exhibited a zooplanktivorous diet and utilised almost exclusively off-shore habitats, in comparison to brown trout which dominated the littoral habitats of both

Table 2 Lifecycle, prevalence (%) and abundance (\pm standard error) of parasites in sympatric Arctic charr *Salvelinus alpinus* (AC) and brown trout *Salmo trutta* (BT) populations in lakes Gangåsvatnet and Våvatnet, southern Norway

| Taxa | Trophically transmitted to fish | 1st intermediate host | 2nd intermediate host | Final host | Gangåsvatnet (153 masl) | | | Våvatnet (300 masl) | | |
|--|---------------------------------|-----------------------|-----------------------|--------------|-------------------------|----------------|------------------|---------------------|------------------|------------------|
| | | | | | BT Littoral | BT Pelagic | AC Profundal | BT Littoral | AC Pelagic | AC Profundal |
| Trematoda | | | | | | | | | | |
| <i>Apatemon</i> sp. | No | Gastropod | Fish | Bird | 0 | 0 | 2.9 | 3.7 | 16.7 | 0 |
| <i>Crepidostomum</i> spp. | Yes | Gastropod, Bivalve | Arthropod | Fish | 12.5 | 7.7 | 0 | 0.1 \pm 0.1 | 0.3 \pm 0.3 | 5.9 |
| <i>Diplostomum</i> sp. | No | Gastropod | Fish | Bird | 0.1 \pm 0.1 | 0.2 \pm 0.2 | 100 | 8.0 \pm 1.5 | 0 | 0.1 \pm 0.1 |
| <i>Phyllostomum umblae</i> | Yes | Gastropod | Arthropod | Fish | 100 | 100 | 100 | 96.3 | 100 | 100 |
| <i>Tylodelphys</i> sp. | No | Gastropod | Fish | Bird | 38.5 \pm 8.0 | 18.2 \pm 5.8 | 106.4 \pm 16.0 | 9.2 \pm 1.6 | 46.7 \pm 9.1 | 52.2 \pm 15.0 |
| | | | | | 93.8 | 69.3 | 97.1 | 96.3 | 100 | 100 |
| | | | | | 5.8 \pm 1.0 | 9.2 \pm 4.8 | 24.2 \pm 2.7 | 13.6 \pm 3.0 | 46.8 \pm 6.8 | 69.7 \pm 7.1 |
| | | | | | 0 | 0 | 2.9 | 0 | 16.7 | 0 |
| | | | | | | | 0.06 \pm 0.06 | | 0.3 \pm 0.3 | |
| Cestoda | | | | | | | | | | |
| <i>Dibothriocephalus</i> spp. | Yes | Copepod | Fish | Bird, Mammal | 93.8 | 92.3 | 100 | 44.4 | 66.7 | 100 |
| <i>Eubothrium crassum</i> ^b | Yes | Copepod | Fish | Bird | 20.3 \pm 5.1 | 16.3 \pm 4.5 | 37.9 \pm 24.0 | 1.3 \pm 0.4 | 3.8 \pm 1.5 | 19.7 \pm 7.1 |
| <i>Eubothrium salvelini</i> ^a | Yes | Copepod | None | Fish | 93.8 | 84.6 | 0 | 0 | 0 | 0 |
| <i>Proteocephalus</i> sp. | Yes | Copepod | None | Fish | 4.7 \pm 1.0 | 3.4 \pm 1.0 | 48.6 | 0 | 83.3 | 82.4 |
| | | | | | 0 | 0 | 0.9 \pm 0.2 | 0 | 2.2 \pm 0.9 | 3.0 \pm 0.8 |
| | | | | | 0 | 0 | 100 | 0 | 100 | 94.1 |
| | | | | | | | 95.6 \pm 17.2 | | 103.0 \pm 33.6 | 149.2 \pm 27.3 |
| Nematoda | | | | | | | | | | |
| <i>Cyathocephalus truncatus</i> | Yes | Unknown | Amphipod | Fish | 0 | 0 | 2.9 | 0 | 0 | 0 |
| | | | | | | | 0.03 \pm 0.03 | | | |
| Copepoda | | | | | | | | | | |
| <i>Argulus</i> sp. | No | None | None | Fish | 6.3 | 15.4 | 8.6 | 0 | 0 | 0 |
| | | | | | 0.1 \pm 0.1 | 0.2 \pm 0.2 | 0.1 \pm 0.1 | | | |
| Number of species | | | | | 6 | 6 | 9 | 5 | 7 | 6 |

^aArctic charr specialist^bBrown trout specialist

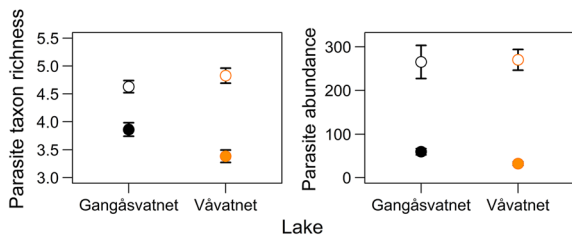


Fig. 1 Differences in parasite taxon richness (number of parasite species per fish; mean \pm standard error) and total parasite abundance (number of individual parasites per fish; mean \pm standard error) between sympatric populations of Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* in lakes Gangåsvatnet and Våvatnet, southern Norway. Note – symbols: lake: black—Gangåsvatnet, orange—Våvatnet; fish species: filled—*S. trutta*, open—*S. alpinus*

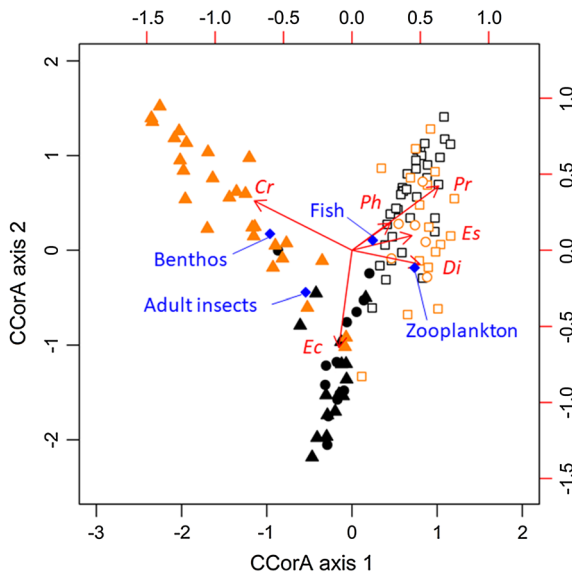


Fig. 2 Relationship between host diet (stomach contents; blue dots) and the trophically transmitted parasite community (red) of sympatric Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* populations in two southern Norwegian lakes. Note – symbols: lake: black—Gangåsvatnet, orange—Våvatnet; fish species: filled—*S. trutta*, open—*S. alpinus*; habitat: triangle—littoral, circle—pelagic, square—profundal; parasite taxon codes: Cr—*Crepidostomum* spp., Ph—*Phyllodistomum umblae*, Di—*Dibothriocephalus* spp., Ec—*Eubothrium crassum*, Es—*E. salvelini*, Pr—*Proteocephalus* sp. Canonical Correlation adjusted $R^2 = 0.27$, $P < 0.001$

lakes. Parasite taxon richness was greater in Arctic charr than brown trout, as predicted by the greater diet breadth and thus potential encounter with parasite intermediate hosts, with parasite abundance in both fish species generally higher in the lower altitude lake

(Gangåsvatnet). Parasite community composition in brown trout from Gangåsvatnet littoral and pelagic habitats was similar, suggesting that although brown trout may move freely between the two habitats, there was still a reliance on prey sources from littoral habitats. Likewise, the parasite community of Arctic charr from both pelagic and profundal habitats in Våvatnet where characterised as taxa trophically transmitted from zooplankton rather than benthos.

Previous studies in Våvatnet (Langeland et al., 1991; L'Abée-Lund et al., 1993) and other southern Norwegian lakes (Sandlund et al., 2016; Jensen et al., 2017) have typically shown Arctic charr to be pelagic zooplanktivores. In contrast, zooplanktivorous Arctic charr in Gangåsvatnet were only caught in profundal habitats (> 20 m), suggesting a degree of daily vertical migration may be occurring to facilitate the observed diet and parasite community. Seasonal vertical migration has been previously observed in Arctic charr, with populations from northern Norwegian lakes known to migrate to upper-open water and littoral habitats during winter (Klemetsen et al., 2003b), whereas populations from southern Norway are often relegated to the profundal habitats during the summer-stratification period (e.g. Jensen et al., 2017), largely due to their preference of water temperatures less than 12°C (Larsson et al., 2005; Siikavuopio et al., 2014). The apparent absence of Arctic charr from pelagic waters of Gangåsvatnet may also be a direct consequence of interactive competition with brown trout, who were also partly zooplanktivorous in the pelagic zone of this lake. Brown trout are typically a benthivore when in sympatry with Arctic charr (e.g. Nilsson, 1963; Klemetsen et al., 2003a, b; Eloranta et al., 2013); however, in a few instances brown trout have been documented to exhibit zooplanktivorous foraging strategies (Klemetsen, 1967; Piggott et al., 2018). Whilst both the habitat and dietary choice observed in this study can be considered “normal” for Arctic charr populations, the presence of zooplanktivore pelagic brown trout was unexpected.

Typically, parasite communities of zooplanktivorous Arctic charr are dominated by copepod transmitted parasites (Knudsen et al., 2008, 2011), as seen in both Våvatnet and Gangåsvatnet Arctic charr populations. However, parasite communities of northern Arctic charr populations are also characterised by parasite species transmitted from benthic prey (Frandsen et al., 1989; Due & Curtis, 1995; Knudsen, 1995), largely attributed

to the greater importance of benthos in their diet in this region (e.g. Knudsen et al., 2010). Furthermore, the overall Arctic charr-parasite taxon richness in the southern Norway study lakes was lower than previously observed in northern Norwegian lakes, due to the absence of a number of trophically- (e.g. nematode *Philonema oncorhynchi* from copepods, *Cystidicola farionis* from amphipods) and directly transmitted taxa (e.g. *Salmincola edwardsii*; Siwertsson et al., 2016; Paterson et al., 2018). In contrast, brown trout parasite communities in Våvatnet and Gangåsvatnet showed greater similarity to those of northern Norwegian brown trout populations (Hartvigsen & Kennedy, 1993; Knudsen et al., 2008; Kristmundsson & Richter, 2009). Although the zooplanktivorous brown trout in Gangåsvatnet were also infected with copepod-transmitted cestodes *Dibothriocephalus* spp. and *E. crassum*, the presence of these parasites may be linked to their predation on paratenic sticklebacks hosts (Curtis, 1984; Williams & Jones, 1994; Kuhn et al., 2016a).

Whilst diet analysis may only represent a snapshot of the diet breadth of each fish, parasites act as long-term tracers of trophic niche (e.g. MacKenzie & Abaunza, 1998). Thus, there is a general consistency among diet, habitat use and the parasite assemblages of fish hosts, as demonstrated by the correlation between the benthos prey-dominated diet of Våvatnet brown trout and *Crepidostomum* spp. infections, for example. In northern Norway, trophic segregation based on trophically transmitted parasites has been observed between sympatric populations of Arctic charr and brown trout in comparative lakes (Knudsen et al., 2008) and inter-individual Arctic charr with different feeding strategies (Knudsen et al., 2010, 2011). However, trophically transmitted parasites have also been shown to reflect consistent differences in trophic niches of polymorphic Arctic charr populations amongst lakes (Siwertsson et al., 2016; Mochetti et al., this volume).

The current study suggests environmental differences over relatively localised spatial scales, in terms of both distance (< 8 km) and altitude (150 m), have the potential to influence the structure of the trophic niche and parasite community of sympatric fish species. Whilst similar patterns are also seen in Arctic charr populations from inter-connected lakes in northern Norway (e.g. 3–105 elevation and 6–8 km distance between lakes; Paterson et al., 2018), the current study demonstrates southern brown trout

populations may also display localised differences in parasite assemblages and diet between lakes. Although previous studies have suggested habitat choice and diet of southern Arctic charr populations may be constrained (e.g. Gregersen et al., 2006; Sandlund et al., 2016; Jensen et al., 2017), our two lake comparison limits our ability to determine whether the observed differences between lakes are related to climatic differences associated with altitude from other factors known to shape fish–parasite assemblages elsewhere (e.g. lake productivity, area; Kennedy, 1978; Finstad et al., 2011). Whilst there is some evidence that Arctic charr populations in low latitude lakes may have lower parasite diversity than their high latitude counterparts (Dorucu et al., 1995; Due & Curtis, 1995; Frandsen et al., 1989; Siwertsson et al., 2016), further studies are required across both altitudinal and latitudinal gradients of sympatric Arctic charr and brown trout populations, especially at lower latitudes, to determine the extent to which also local climate-induced gradients may be responsible for shifting the diet niche and parasite communities.

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