Latitudinal distribution and abundance of the trematode parasites *Rhipidoctyle fennica* and *R. campanula*

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Aim
We studied two trematode parasites, *Rhipidoctyle fennica* and *R. campanula*, and their duck mussel (*Anodonta anatina*) host, at high latitudes, close to the northern limit of their occurrence, in order to evaluate the roles of host availability and transmission factors in determining the distribution and abundance of the parasites. A previous study showed that *R. campanula* started cercarial larvae production immediately after the water temperature had increased to 15 °C, but *R. fennica* only 35-45 days later. Thus, we hypothesized that the abundance of *R. fennica* relative to that of *R. campanula* should decrease with latitude due to the constrained transmission of the former at northern, cold, short summer habitats (transmission hypothesis).

Location
Finland with focus on three regions along a latitudinal gradient; south (61-64 °N), low north (65-66 °N) and high north (67-69 °N).

Methods
Parasite and host data were collected from 37 southern, 13 low northern and 7 high northern water bodies, and temperature data from throughout the country. Frequency of occurrence of the duck mussel was used as a measure of host availability, and the number of days with the mean air temperature ≥ 15 °C (15C-days) was used as a measure of transmission potential.

Results
Number of 15C-days was mostly 41-60 in the south, 21-40 in the low north and ≤ 20 in the high north region. *R. fennica* declined from south to low north, but no difference between south and low north was observed in the frequency of occurrence of *R. campanula* or the duck mussel host. However, both *Rhipidocotyle* parasites and their duck mussel host were absent from the high north region.

Main conclusions
Transmission constraint due to the short summer probably limits the northern range of *R. fennica*. Lack of the duck mussel host probably determines the northern range border of *R. campanula*.

Key words: *Anodonta*, Arctic, climate change, distribution, host availability, latitude, parasite, temperature, transmission

INTRODUCTION

Most free-living animal taxa decrease in diversity with increasing latitude (e.g., MacArthur, 1972; Rosenzweig, 1995; Willig *et al.*, 2003). Parasite species richness has also been found to decrease with increasing latitude in several host groups including fish (Rohde, 1982; Rohde & Heap, 1998; Choudhury & Dick, 2000; Poulin, 2001), crustaceans (Thieltges *et al.*, 2009), primates (Nunn *et al.*, 2005) and humans (Guernier *et al.*, 2004; Cashdan, 2014). However, some studies show an opposite pattern: trematodes of marine gastropods, helminths of primates and parasites of carnivores increased in diversity with increasing latitude (Poulin & Mouritsen 2003; Nunn *et al.*, 2005; Lindefors *et al.* 2007). On the other hand, no dependence between latitude and trematode species richness was found in the European fresh water fish (Thieltges *et al.*, 2011). A recent meta-analysis by Kamiya *et al.* (2014) indicated that the relationship between parasite species richness and latitude is weak, but mainly positive, with richness increasing with latitude. Thus, the latitudinal gradients in parasite diversity may differ from those of free-living taxa, and more research especially on the factors influencing latitude dependence of parasite species occurrence is required (Kamiya *et al.*, 2014).

It has been shown that climate factors, most importantly temperature, contribute to fish species diversity, with decline in richness towards higher latitudes (Griffiths *et al.*, 2014). Therefore, the diversity of fish parasites should also, in theory, decline with latitude since parasite diversity depends on host diversity (Watters, 1992, Hechinger & Lafferty, 2005, Krasnov *et al.*, 2007). The possible decline in parasite species richness at high latitudes could partly result from colonization history or development/transmission constraints. In the northern hemisphere, parasite species or their hosts may not have had enough time to recolonize the high northern areas after the last glaciation. Alternatively, the climatic conditions at high latitudes may be unfavourable for the development and transmission of the parasite or for the development of the host(s). The roles of host availability and transmission factors in determining the geographic patterns of parasite species distribution and abundance are not well known. Global climate warming will inevitably affect distribution and abundance of both hosts and parasites in the future (Marcogliese, 2001; Harvell, *et al.*, 2002; Lafferty, 2009). Therefore, better knowledge of the factors that contribute to the biogeography of parasites will be essential in order to predict the anticipated outcome of climate warming for different parasite species.

Taskinen *et al.*, (1991) and Gibson *et al.*, (1992) described life cycles of the two bucephalid trematodes, *Rhipidocotyle fennica* and *R. campanula*. In northernmost Finland the hosts of these *Rhipidocotyle* species are close to the limit of their geographic distribution. The first intermediate host for both *Rhipidodocotyle* parasites, the bivalve mollusc *Anodonta anatina* and the common second intermediate host fish, roach) *Rutilus rutilus*), have been found up to latitude 68°N (Oulasvirta *et al.*, 2008; Hayden *et al.*, 2013). The definitive hosts for *R. fennica* and *R. campanula*, northern pike (*Esox lucius*) and European perch

(*Perca fluviatilis*) respectively, occur throughout Finland up to 70°N, although more sporadically and in low numbers at the highest latitudes (Hayden *et al,*. 2013; 2014). Later Taskinen *et al*. (1991) reported that the cercarial shedding by *R. campanula* responds quickly to increasing temperature, but that by *R. fennica* is much slower. Consequently, under field conditions *R. campanula* starts seasonal cercarial emission 3-4 weeks earlier (early June vs. late July) and at a lower temperature than *R. fennica* (Taskinen *et al.,* 1994, Taskinen 1998a). Cercarial release by *R. campanula* started almost immediately as water temperature reached 15 °C, whereas emergence of *R. fennica* cercariae only started 30 to 45 days later (Taskinen *et al.,* 1994). These results were experimentally confirmed in a long-term temperature manipulation study (Choo and Taskinen, unpublished). Thus, transmission of *R. fennica* should be more severely temperature-constrained in high latitude, cold, short-summer habitats, than that of *R. campanula*.

We studied the latitudinal distribution and abundance of the *Rhipidoctyle* parasites and their first intermediate bivalve host (*Anodonta antina*) at their northern boundary of distribution. Frequency of occurrence of *A. anatina* was used as a measure of host availability, and the number of days with mean air temperature ≥ 15 °C (15C-days) was used as a measure of transmission potential. As the critical length of the warm (≥ 15 °C) period for cercarial production by *R. fennica* is 30-45 days (Taskinen *et al*. 1994), our hypothesis was that (i) the northernmost occurrence of *R. fennica* would be in the zone of 30-45 15C-days. In addition, we hypothesised that (ii) the abundance of *R. fennica* relative to that of *R. campanula* should decrease with latitude due to the constrained transmission at northern, cold, short-summer habitats. We further hypothesised that (iii) transmission factors should constrain the occurrence of *R. campanula* only if the number of 15C-days is very low. On the other hand, lack of the obligatory host (and the parasites) from a given region would indicate host availability as a decisive factor contributing to the biogeography of the parasites.

MATERIALS AND METHODS

We mapped the occurrence, prevalence and the abundance of *R. fennica* and *R. campanula* in their first and second intermediate hosts, the duck mussel (Unionidae) and roach (Cyprinidae), respectively, in three regions along a latitudinal gradient: south (61-64 °N), low north (65-66 °N) and high north (67-69 °N) (Fig. 1). In addition, we investigated the occurrence of the duck mussel by examining roach and perch for presence of parasitic glochidium larvae of the mussel, as these fish are suitable hosts for *A. anatina* glochidia (Jokela *et al.,* 1991). The northernmost site of the low north region, the River Kemijoki (Table 1), is located on the Arctic Circle. All the high north sites can be regarded as

belonging to the Arctic, whereas the low north and the south regions belong to the Northern temperate zone.

Materials were collected from 57 water bodies; 37 south, 13 low north and 7 high north lakes and rivers, belonging to 10 catchments (Table 1). All the sites are in Finland except for the River Patajoki, Sweden (site 55, high north). Eight of the catchments (53 sites) drain into the Baltic Sea. Two catchments drain into the White Sea (catchments 7 and 8, sites 46-49, Table 1, Fig. 1). The proportion of lakes vs. rivers among the studied water bodies (84, 92 and 86 % in the south, low north and high north, respectively) did not differ between regions (χ^2-test, $P = 0.748$). Nor did the median (min-max) surface area of the south, low north and high north lakes [3.0 (0.02-1081), 4.0 (0.03-273) and 0.9 (0.27-6.9) km^2, respectively] differ between regions (Kruskall-Wallis test, test statistics = 1.420, $P= 0.492$). Material was collected between 1989 and 2015, so that the south and low north sites were sampled earlier (1989-2015) than the high north sites (2013-2015) (Table 1).

Duck mussels were collected from 29 of the 57 water bodies (Table 1), and examined for *R. fennica* and *R. campanula*. Roach plus perch were caught from 19 water bodies, while from eight water bodies, only perch were caught (Table 1). Only roach was collected from the River Patojoki. When *R. fennica* or *R. campanula* were found either in the duck mussel or in roach, the parasites were recorded as occurring in that water body. Similarly, if duck mussel glochidia were found from either roach or perch, or both species, duck mussel was recorded as occurring in that site.

Fish were collected by ice-fishing between February and April (except for the River Patojoki, which was sampled in October using a fish trap) because glochidia of duck mussel in fish are found in winter in this area (Jokela *et al.*, 1991) and since no marked seasonal changes in the prevalence and the intensity of *Rhipidocotyle* parasitism in roach takes place during the ice-covered winter months (Taskinen *et al.* 1994). When using the fish data to study the geographic occurrence of the duck mussel, the River Patojoki site, sampled in October, was excluded because that is not a suitable time to find the glochidia of duck mussel (Jokela *et al*. 1991). Fishes were euthanized with a sharp blow to the head, stored and transported on ice to the laboratory. Fish were measured for length and the fins of roach were examined for *R. fennica* metacercariae and duck mussel glochidia, and the gills of roach were examined for *R. campanula* metacercariae and mussel glochidia, while fins and gills of perch were examined for duck mussel glochidia (Jokela *et al.*, 1991, Taskinen *et al.* 1991). Mean site-specific length of roach differed between the three latitudinal regions (log-transformed length, one-way ANOVA, $F_{2, 21} = 7.403$, $P = 0.004$). Tukey's B post hoc test indicated that the south (12 water bodies) and the low north (7 water bodies) areas formed a homogenous subset with no difference in the average fish size (mean ± s.e; 145.8 ± 3.1 and 152.1 ± 3.3 mm, respectively), but roach from the high north region (five water bodies) were significantly larger (177.4 ± 4.0 mm). Mean site-specific length of perch differed significantly between the three regions (one-way ANOVA, $F_{2, 26} = 19.312$, $P < 0.001$). Tukey's B post hoc test

indicated that all pair-wise differences between latitudes were significant ($P < 0.05$). Hence the mean (± s.e.) site-specific mean length of perch increased from the south (119.8 ±2.5 mm, 16 water bodies) to the low north (136.2 ± 4.2 mm, seven water bodies) and to the high north (151.8 ± 5.9 mm, six available locations).

Duck mussels were randomly collected by hand picking, snorkelling or SCUBA diving and transported alive to the laboratory. Mussels were measured for length and age (growth rings on the shell), and examined microscopically for *Rhipidocotyle* sporocysts by pressing pieces of the gonad tissue between two large glass plates and viewing with transmitted light (Taskinen *et al.* 1991). The duck mussels were collected during the summer; seasonal changes in the prevalence of *Rhipidocotyle* parasitism in duck mussels are not significant (Taskinen *et al.* 1994). Mean (± s.e.) site-specific age of mussels was lower in the 22 southern water bodies (5.2 ± 0.3 y) than in the six low north sites (8.5 ± 0.4 y) (mussels were not available from the high north region) (One-way ANOVA, $F_{1, 26} = 24.996$, $P < 0.001$). Average (± s.e.) site-specific mean length of mussels was also lower in the south (67.1 ± 2.2 mm) than in the low north (77.1 ± 4.8 mm) materials (One-way ANOVA, $F_{1, 26} = 4.342$, $P < 0.047$).

Using meteorological data from 1961-2014, a map was constructed with the number of days when the daily mean air temperature was ≥ 15 °C (Fig. 1) in order to evaluate the length of the seasonal transmission window of the parasites. Climatological data on the mean daily air temperatures were obtained from the Finnish Meteorological Institute database.

Differences between the three regions in the frequency of water bodies occupied by *R. fennica*, *R. campanula* or duck mussel (glochidia) were analysed using χ^2 test or Fisher's exact test. Differences in the site-specific infection prevalences, infection abundances, ages and lengths between the latitudinal regions were analysed using one-way ANOVA and Tukey's B post hoc tests, using site-specific mean values. If the assumptions of ANOVA were not met, even after log-transformation of the response variable, non-parametric tests were used. Relationship between latitude and the prevalence or mean abundance of *Rhipidocotyle* species was studied using Spearman rank correlation analysis. To account for multiple tests, the Bonferroni correction was applied to p-values.

RESULTS

Geographic variation in air temperatures

The average length of the period when the mean daily air temperature was ≥ 15 °C ranged from > 60 days in southernmost Finland to less than 10 days in the north (Fig. 1). Southern sites belonged mainly to the 41-50 and 51-60 d zones, while one southern site experienced > 60 d of ≥ 15 °C. With one exception, the low north sites belonged to 21-30 and 31-40 d of ≥ 15 °C zones. With one

exception, the high north sites belonged to the 11-20 d of ≥ 15 °C zone (Fig. 1). The average seasonal period when air temperature is ≥ 15 °C was about 20 days longer in the southern sites than in the low north sites, and 10 days longer in the low north than in the high north sites.

Occurrence of R. fennica *and* R. campanula *in the combined mussel and fish data*

Both parasites occurred in the southernmost site of the study, River Kymijoki in Kuusankoski (site 1, 60° 99′ N, Table 1, Fig. 1), where the prevalence of infection in the duck mussel was 46.8 and 3.4 % for *R. fennica* and *R. campanula*, respectively. The most northerly site where *R. fennica* occurred was Lake Siikalampi (site 39, 65° 58′ N, Table 1), with 9.1 % of the duck mussels infected. The northernmost occurrence of *R. campanula* was in the River Kemijoki (site 50, 66° 33′ N, Table 1, Fig. 1), with 2.2 % of the duck mussels infected. Thus, in the northernmost temperature zones where *R. fennica* and *R. campanula* occurred, the mean durations when the air temperature was ≥ 15 °C were 31-40 and 21-30 days, respectively.

The frequency of occurrence of *R. fennica* was significantly higher in the south (25 out of 32 sites, 78%) than in the low north (one out of 12 sites, 8%) (Fisher's exact test, $P < 0.001$) (Fig. 2). *R. fennica* was not found in any of the five available high north water bodies, and the difference between the low and the high north regions was not significant (Fisher's exact test, $P = 1.000$). In the case of *R. campanula*, the frequency of occurrence was almost equal in the south (21 out of 32 water bodies, 66 %) and the low north (8 out of 12, 67 %) region. However, the difference in the frequency of occurrence of *R. campanula* between the low north and the high north, where *R. campanula* did not occur in any of the five sites studied, was statistically significant (Fisher's exact test, $P = 0.029$) (Fig. 2).

No catchment-specific differences were evident within the southern region. *R. fennica* and *R. campanula* occurred in all of the three southern catchments, and there was no difference between the catchments with regards to the frequency of occurrence of *R. fennica* (χ^2 test, $P = 0.212$) and *R. campanula* (χ^2 test, $P = 0.253$). In the low north region, *R. fennica* occurred only in one site, which belongs to the River Iijoki catchment, but *R. campanula* was found in five of the six catchments studied. Moreover, in the low north region, *R. campanula* occurred in all the catchments draining to the Baltic Sea, and in one (River Vienan Kemijoki) of the two catchments that drain into the White Sea. The River Kemijoki catchment was the only one to run through two regions, low north and high north. There *R. campanula* was observed in site 50 (66° 33′ N), low north, but not in the more northerly high north water bodies (sites 52-54, 68° 39-44′ N, Table 1). The catchments from which *Rhipidocotyle* parasites were not found included the River Koutajoki (sites 47 and 48, White Sea drainage) and the River Tornionjoki (sites 55-57, Baltic Sea drainage).

Occurrence of the duck mussel host

Duck mussel glochidia were found in eight (57 %) of the 14 southern sites, in six (86 %) of the seven low north sites and in none of the six high north locations (Fig. 2). The difference between the south and low north regions was not significant (Fisher's exact test, P = 0.660), but the decline in the frequency of occurrence of duck mussel from the low north to the high north region was statistically significant (Fisher's exact test, $P_{\text{Bonferroni corrected}}$ = 0.010). The River Kemijoki, low north (site 50, 66° 33′ N, Table 1, Fig. 1) was the northernmost waterbody where the duck mussel was found.

Mean prevalence of R. fennica *and* R. campanula *in the duck mussel*

Duck mussels were found only from the south and low north regions. Mean prevalence of *R. fennica* infection in the duck mussel was significantly higher in the 23 southern sites than in the six low north sites (Mann-Whitney U = 25.00, P = 0.016) (Fig. 3). There was a significant negative correlation between latitude and the prevalence of *R. fennica* infection in the duck mussel over the south and low north regions (Spearman's rho = -0.511, P = 0.005, n = 29).

In contrast, the mean prevalence of *R. campanula* infection in the duck mussel did not differ between the south and low north (Mann-Whitney U = 93.00, P = 0.212) (Fig. 3). In addition, there was no relationship between latitude and the mean prevalence of infection by *R. campanula* over the south and low north regions (Spearman's rho = -0.204, P = 0.290, n = 29).

The mean ± s.e. difference (*R. fennica* minus *R. campanula*) in the site-specific prevalence of the parasites in the duck mussel was +15.5 ± 4.0 % (thus, in favour of *R. fennica*) in the south and -5.1 ± 2.0 % (in favour of *R. campanula*) in the low north. This difference was statistically significant (One-way ANOVA, $F_{2, 17}$ = 6.800, P = 0.015).

Mean abundance of R. fennica *and* R. campanula *in roach*

The average site-specific mean abundance of *R. fennica* in roach was 58, 0.3 and zero metacercariae fish^{-1} in the 12 available southern, seven low north and five high north water bodies, respectively (Fig. 4). The decrease in the abundance of *R. fennica* from the south to the low north was statistically significant (Mann-Whitney U = 38.00, P = 0.005), but the abundances of *R. fennica* in the low north and high north regions did not differ (Mann-Whitney U = 15.900, P = 0.755). When the relationship between latitude and *R. fennica* abundance was studied over the whole roach material, there was a significant decrease in infection abundance with latitude (Spearman's rho = -0.717, P < 0.001, n= 24).

The average mean ± s.e. abundance of *R. campanula* in roach was equal in the south and low north latitudes (Fig. 4), respectively, but zero in the high north. The mean abundance of *R. campanula* decreased significantly from the low north to high north region (Mann-Whitney U = 5.00, P = 0.048). Over the whole geographic area of the study, *R. campanula* abundance decreased significantly with latitude (Spearman's rho = -0.603, P = 0.002, n= 24).

The mean ± s.e. difference (*R. fennica* minus *R. campanula*) in the abundance of the parasites in roach was +41.8 ± 15.8 metacercariae fish^{-1} (thus

in favour of *R. fennica*) in the south and -16.1 ± 12.1 metacercariae fish^{-1} (in favour of *R. campanula*) in the low north, the difference being statistically significant (One-way ANOVA, $F_{2, 17}$ = 6.427, *P* = 0.021).

DISCUSSION

In our large scale study of 57 sampling sites, the frequency of occurrence, the mean prevalence and the average site-specific mean abundance (in both duck mussel and roach) of *R. fennica* decreased from the south to the low north region, but this pattern was not detected in *R. campanula*. Moreover, both *Rhipidodcotyle* parasites, and their first intermediated host, the duck mussel, were completely absent from the high north region.

How can the transmission hypothesis explain the geographic range of *R. fennica* and *R. campanula*? In a previous study, emergence of *R. fennica* cercariae started only 30 to 45 days after the rise of water temperature to 15 °C (Taskinen *et al.*, 1994). As expected, the zone of 31-40 15C-days was the northernmost temperature zone where *R. fennica* was found (Lake Siikalampi, site 39, low north). It is possible that beyond the zone of 31-40 15C-days the short summer and low temperature will constrain the cercarial production, and hence the transmission, of *R. fennica*. In the high north region, the prevailing temperature conditions should strongly limit the occurrence of *R. fennica*, as there was mostly only 11-20 days with air temperature ≥ 15 °C.

In addition, the general occurrence frequency of *R. fennica* in water bodies, as well as the mean prevalence of *R. fennica* infection in the duck mussel and the average mean abundance of *R. fennica* metacercariae in roach, were lower in the low north than in the south. This could also be explained by the transmission (larval release) hypothesis, i.e. the shorter warm water period in the low north region. The only site where *R. fennica* was found in the low north region, Lake Siikalampi, is a shallow pond, presumably a warmer-than-average habitat.

In a previous study by Taskinen *et al.* (1994), *R. campanula* started cercarial release almost immediately after the water temperature had increased to 15 °C. Thus, if the water temperature corresponds to that of air, it is reasonable to assume that occurrence of *R. campanula* is not constrained by cercarial release in any of the present geographic areas, not even in the high north where mostly more than 20 days with ≥ 15 °C was observed. Consistent with this, there was no difference in the occurrence frequency, in the mean prevalence in duck mussel or in the average mean abundance in roach, of *R. campanula* between the south and the low north. Thus, the transmission hypothesis cannot necessarily explain the lack of *R. campanula* from the high north, although it can explain the geographic occurrence of *R. fennica*.

How might the host availability hypothesis then explain the geographic range of the parasites? The molluscan host of *Rhipidocotyle* parasites, duck mussel, did not occur in any of the high north sites. Therefore, host availability may well explain the lack of *Rhipidocotyle* spp. in the high north region. Duck mussel is the only suitable mussel host available for *Rhipidocotyle* parasites in

these latitudes; other unionids have not been found to serve as a host for *Rhipidocotyle* species here (Taskinen *et al.,* 1991) and the distribution of other unionid mussels in northern Europe is more southerly than that of the duck mussel, *A. anatina* (Lopes-Lima *et al.,* 2015). In the present study, *R. campanula* occurred as far north as its host, the duck mussel, i.e. in the River Kemijoki, low north (at the Arctic Circle, 66° 33′ N, site 50, Table 1).

The high north sites were located in two major drainages, the River Kemijoki and the River Tornionjoki (catchments 9 and 10, Table 1). These catchments are both occupied by duck mussel, as shown by this study and Oulasvirta *et al*. (2008), respectively. The southern part of the River Kemijoki catchment, at least in the main channel of the river, is also occupied by *R. campanula*. In northern Finland, higher latitude is generally associated with increase in altitude because of the Scandinavian Mountains. Therefore, in addition to the latitudinal gradient there is also an altitudinal gradient in the present study area, and many of the high north sites are also of higher altitude. The high north sites, located at higher altitudes in the headwaters, are presumably less readily colonized by host fishes of duck mussel and *Rhipidocotyle* species. However, duck mussel has earlier been reported as far north as 68° N, in the headwaters of the River Tornionjoki watershed (Oulasvirta *et al.,* 2008), one of our high north catchments.

There was a temporal mismatch in the collection of materials, as the high north sites were sampled later than the other regions. However, that should have increased, rather than decreased, the probability of occurrence of the parasites in the north since the ongoing climate warming has increased the annual mean temperature and the length of summer in this region (Mikkonen *et al*. 2014).

In the southern latitudes, the average abundance of *R. fennica* in roach was about 40 metacercariae fish^{-1} higher than that of *R. campanula*. This could be explained by the clearly higher cercarial production by *R. fennica* (9.500 larvae day^{-1}) than by *R. campanula* (1.400 cercariae day^{-1}) at 20 °C observed previously in the south region of the present study (Taskinen *et al.,* 1991).

There was no difference between the southern catchments with respect to occurrence of *R. fennica* and *R. campanula*. Two catchments in the northern areas did not have either of the *Rhipidocotyle* species, the River Tornionjoki (three high north sites, Baltic Sea drainage) and the River Koutajoki (two low north sites, White Sea drainage). In the River Tornionjoki area, this is probably connected to the northern location of the study sites; high north sites were not inhabited by *Rhipidocotyle* spp. regardless of catchment. That only two sites were sampled from the River Koutajoki catchment may have contributed to the apparent absence of *Rhipidocotyle* spp., since it belongs to the low north region which does harbour *Rhipidocotyle* parasites. Nor should belonging to the White Sea drainage rule out the occurrence of *Rhipidocotyle* spp., as *R. campanula* was observed in the River Vienan Kemijoki catchment, also flowing to the White Sea. Hence at least *R. campanula* has colonized the White Sea drainage, although the core distribution range of *Rhipidocotyle* parasites may be the Baltic Sea

drainage area (Taskinen *et al.,* 1991; Müller *et al.,* 2014; Petkevičiūtė *et al.,* 2014; Stunžėnas *et al.,* 2014).

Climate models predict a 2 to 7° C increase in annual temperature in Finland by the 2080s, compared to a 1961-1990 baseline period (Jylhä *et al.,* 2004). Climate warming is predicted to affect the global distribution of parasites, with range expansion or shift towards higher latitudes (Marcogliese, 2001; Harvell, *et al.,* 2002; Lafferty, 2009; Laaksonen *et al.* 2010). Thus, climate warming will inevitably also change the northern distribution of the *Rhipidocotyle* parasites. Based on the present results, and the observed need for high temperature and a long warm period for the cercarial release by *R. fennica* (Taskinen *et al.,* 1994), the first change to take place will probably be an increase of *R. fennica* in the low north region due to the longer and warmer summers predicted. The next change can be the expansion of the core distribution area for duck mussel to the high north region, accompanied with colonization of the area by *R. campanula*. Later, the high north region would probably also be colonized by *R. fennica*.

Currently the high north populations of roach are living without *Rhipidocotyle* parasites. As the present results show, the numbers of *R. fennica* and *R. campanula* can be as high as 1024 and 180 metacercariae fish^{-1} with mean abundances of 194 and 63 parasites fish^{-1} lake^{-1}. Parasites of the family Bucephalidae, including *Rhipidocotyle*, can severely harm their fish host, and even cause mass mortality in their cyprinid hosts under stressful conditions (Hoffman *et al.,* 1990). Therefore, both the current lack of *Rhipidocotyle* parasites from roach in the northernmost water bodies and the anticipated spread of these parasites to those habitats in the future climate can be expected to have an important influence on roach individuals and populations in northern latitudes. In addition, both *Rhipidocotyle* species decrease the growth, survival and reproduction of the duck mussel (Taskinen & Valtonen, 1995; Taskinen, 1998b; Jokela *et al.,* 2005; Müller *et al.,* 2014). Therefore, the current low frequency of occurrence of *R. fennica* in the low north, and the predicted increase of the species there in the future, should have a major impact on the duck mussel individuals and populations in northern latitudes. As roach and mussels can have important roles in their ecosystems (e.g., Jeppesen *et al.,* 2010; Vaughn *et al.,* 2008), lack or spread of these organisms from/to the high north region have also potential ecosystem level consequences.

Our results suggest that i) the low occurrence, prevalence and abundance of *R. fennica* in the low north region can be explained by the possible transmission constrain, while ii) the lack of *R. fennica* and *R. campanula* from the high north may be explained by host availability, as the obligatory host, duck mussel, was also missing from the high north sites. Arctic and Subarctic regions may offer good models for studying the impacts of climate change on parasite ecology because they are generally simple systems with few other, confounding anthropogenic factors (Kutz *et al.,* 2009). Thus, our study will provide a baseline for future monitoring of the geographic distribution of these parasites and their hosts at high latitudes in warming climates.

Acknowledgements

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Table 1. Study lakes (L.) and rivers (R.), study site number (#),catchments (C), lake surface area (km²), latitude (Lat.), longitude (Long.), numbers of individuals studied and year of collection (n/year), mean age (y) of duck mussels and mean length (mm) of mussels and fishes (roach and perch).

	#	C	Area	Lat.	Long.	Duck mussel			Roach		Perch	
						n/year	Age	L	n/year	L	n/year	L
South												
R. Kuusankoski	1	1		60.90	26.62	177/1996	-	-	-	-	-	-
L. Saraavesi	2	1	10.5	61.51	25.99	85/1996	6.1	64.9	90/1989[a]	-	-	-
L. Särkijärvi	3	1	0.04	61.93	27.71	-	-	-	-	-	10/1996	128.3
L. Päijänne	4	1	1081	61.93	25.54	142/2012	4.0	71.2	15/1996	173.3	15/1996	145.1
L. Huhtalampi	5	1	0.16	62.06	26.27	-	-	-	-	-	15/1996	109.7
L. Pettämä	6	1	9.00	62.06	25.16	100/2014	7.0	68.8	-	-	-	-
L. Valkonen_1	7	1	0.03	62.21	25.51	-			-	-	15/1996	118.8
L. Iso-Kairahta	8	1	0.16	62.22	25.91	42/1996	7.4	70.8	-	-	-	-
L. Valkonen_2	9	1	0.06	62.22	25.58	-	-	-	-	-	15/1996	124.1
L. Leppävesi	10	1	64.0	62.23	25.96	-	-	-	15*/1996	130.9	15*/1996	118.1
L. Jyväsjärvi	11	1	3.00	62.23	25.74	161/1996	6.1	61.1	15/1996	149.2	11/1996	113.6
R. Myllylänjoki	12	1		62.23	24.87	60/2014	6.3	62.5	-	-	-	-
L. Palokkajärvi	13	1	2.58	62.26	25.75	12/1996	4.8	52.1	-	-	-	-
L. Tuomiojärvi	14	1	2.98	62.26	25.74	55/1996	5.8	55.0	-	-	-	-
L. Vuorilampi	15	1	0.02	62.26	25.69	-	-	-	-	-	15/1996	113.1
L. Ala-Kintaus	16	1	7.00	62.28	25.33	-	-	-	15/1996	148.6	15/1996	125.1
L. Alvajärvi	17	1	2.09	62.32	25.73	154/1996	7.0	65.4	-	-	-	-
L. Kuuhankavesi	18	1	19.0	62.38	26.42	-	-	-	15*/1996	148.6	15*/1996	113.3
L. Vuojärvi	19	1	0.73	62.42	25.93	7/1996	4.7	55.0	-	-	-	-
L. Ahveninen	20	1	1.57	62.44	25.99	57/1996	4.2	45.1	-	-	-	-
R. Kuusaankoski	21	1		62.46	25.95	168/1996	4.9	77.7	-	-	-	-
L. Kuusvesi	22	1	22,00	62.47	26.03	-	-	-	15*/1996	134.3	15*/1996	109.5
L. Uurainen	23	1	13,00	62.53	26.07	-	-	-	-	-	15/1996	112.8
R. Pesiäissalmi	24	1		62.57	26.24	54/1996	4.4	60.9	-	-	-	-
L. Konnevesi	25	1	189	62.58	26.45	-			15*/1996	152.5	15*/1996	134.6
R. Siikakoski	26	1		62.62	26.34	37/1996	7.1	64.4	-		15/1996	115.3
L. Kivijärvi	27	1	154	63.03	25.13	-	-	-	15*/1996	146.0	15*/1996	112.6
L. Keitele	28	1	494	63.19	25.60	-	-	-	15*/1996	142.5	15*/1996	122.4
L. Katumajärvi	29	2	3.78	60.99	24.51	41/2013	5.8	74.0	-	-	-	-

L. Vanaja	30	2	0.76	60.99	24.47	50/1996	4.1	80.9	-	-	-	-
R. Moisionjoki	31	2		61.38	23.78	51/1996	6.3	78.9	-	-	-	-
L. Suolijärvi	32	2	2.03	61.44	24.80	19/2013	3.6	69.3	-	-	-	-
L. Keurusselkä	33	2	118	62.22	24.70	-	-	-	15/1996	140.0	-	-
L. Koijärvi	34	3	0.27	61.89	29.20	71/2005	2.7	81.8	-	-	-	-
L. Haukivesi	35	3	560	62.07	28.61	41/2005	7.0	69.1	-	-	-	-
L. Valkeinen	36	3	0.10	62.89	27.67	50/2005	2.5	83.6	-	-	-	-
L. Ala-Haajainen	37	3	1.19	63.63	26.99	43/2006	3.5	64.4	-	-	-	-
Low North												
L. Kuivasjärvi	38	4	0.82	65.07	25.47	107/1996	9.5	93.2	12/1989[a]	150.0	-	-
L. Siikalampi	39	5	0.38	65.58	28.25	72/1996	8.4	82.0	-		-	-
L. Iso-Kero	40	5	61.3	65.68	29.12	-	-	-	15*/2014	164.2	15*/2014	138.5
L. Vähäjärvi	41	5	0.99	65.75	29.14	-	-	-	15*/2014	140.4	15*/2014	134.4
L. Yli-Kuoliojärvi	42	5	1.53	65.82	28.84	-	-	-	20*/2014	145.6	15*/2014	134.7
L. Ranuanjärvi	43	5	4.62	65.92	26.58	72/1996	8.1	62.3	-	-	-	-
L. Aimolampi	44	5	0.03	66.03	27.86	-	-	-	-	-	15/2014	159.7
L. Hyrynjärvi	45	6	18.0	64.72	28.55	140/1996	8.5	85.0	-	-	-	-
L. Posionjärvi	47	7	18.9	66.13	28.13	-	-	-	30*/2014	146.4	15*/2014	127.0
L. Yli-Kitka	48	7	273	66.14	28.64	-	-	-	15*/2014	160.0	15*/2014	126.5
L. Oivanginjärvi	46	8	3.38	66.04	29.05	98/1996	9.7	73.5	-	-	-	-
L. Kuusamojärvi	49	8	47.4	65.93	29.27	-	-	-	15*/2014	157.9	15*/2014	132.5
R. Kemijoki	50	9		66.33	27.67	60/1996	6.8	66.8	-	-	-	-
High North												
L. Ounasjärvi	51	9	6.93	68.38	23.64	-	-	-	17*/2014	208.4	15*/2014	164.7
L. Angelijärvi	52	9	0.33	68.39	24.19	-	-	-	20*/2014	150.8	15*/2014	169.7
L. Venejärvi	53	9	0.86	68.41	24.44	-	-	-	15*/2014	159.1	15*/2014	146.9
L. Vuontisjärvi	54	9	0.92	68.44	24.00	-	-	-	41*/2014	154.1	15*/2014	140.5
R. Patojoki	55	10		67.39	23.40	-	-	-	10/2014	210.4	-	-
L. Leppäjärvi	56	10	0.27	68,52	23.31	-	-	-	-	-	15*/2014	132.6
L. Palojärvi	57	10	3.62	68.59	23.36	-	-	-	-	-	15*/2014	156.6

Catchments: 1, River Kymijoki; 2, River Kokemäenjoki; 3, River Vuoksi/Neva; 4, River Kuivasoja; 5, River River Iijoki; 6, River Oulujoki,; 7, River Koutajoki; 8, River Vienan Kemijoki; 9, River Kemijoki; 10, River Tornionjoki

* ice-fishing competition, tens or hundreds of fishermen, hundreds or thousands of fish collected
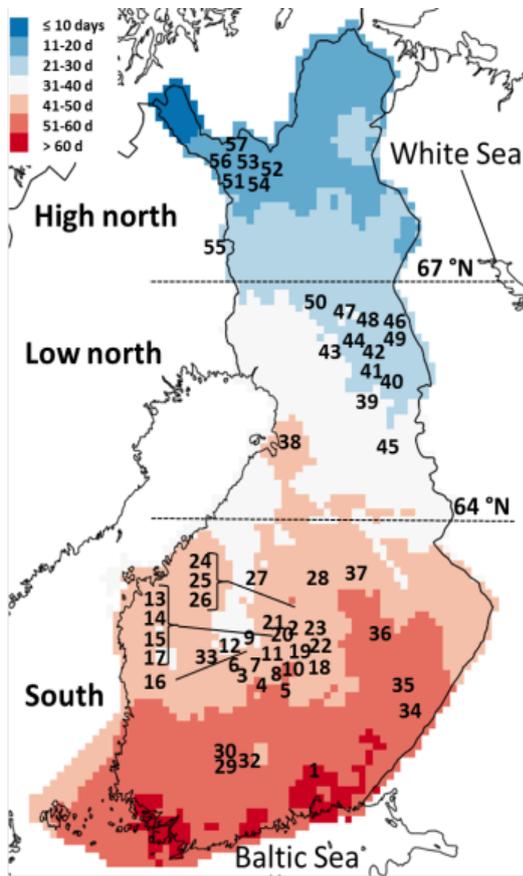
[a] from Taskinen *et al.* 1991

Figure 1. Geographic location of the study sites from 1 to 57 (see Table 1 for details) and the temperature zones (number of days when daily mean temperature ≥ 15 °C) within Finland.
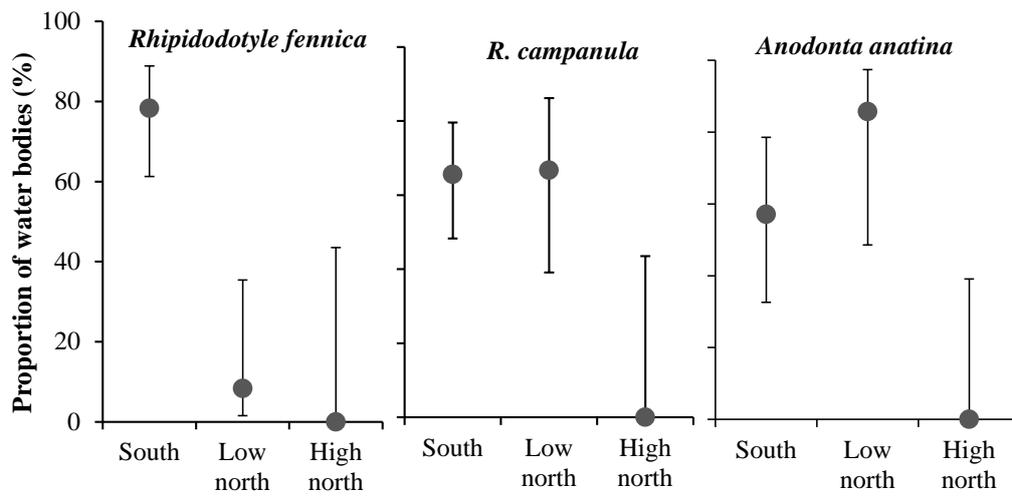
Figure 2. Mean (± 95 % confidence interval) frequency of occurrence of the parasites *Rhipidocotyle fennica* and *R. campanula*, and their first intermediate host, duck mussel (*A. anatina*), in the south, low north and high north regions.
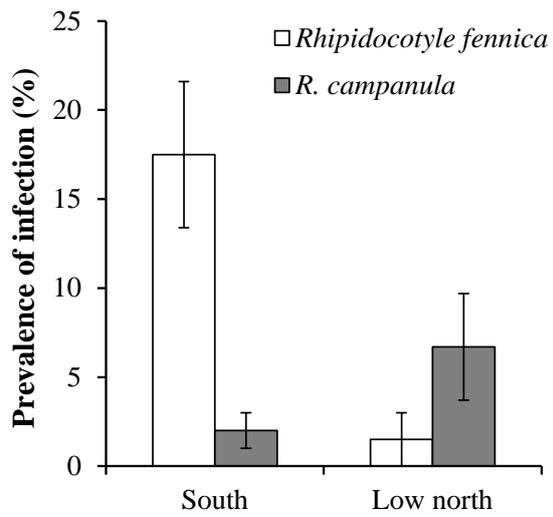
Figure 3. Mean (± s.e.) prevalence of infection of the parasites *Rhipidocotyle fennica* and *R. campanula* in their first intermediate mussel host, duck mussel, in the south and low north regions.
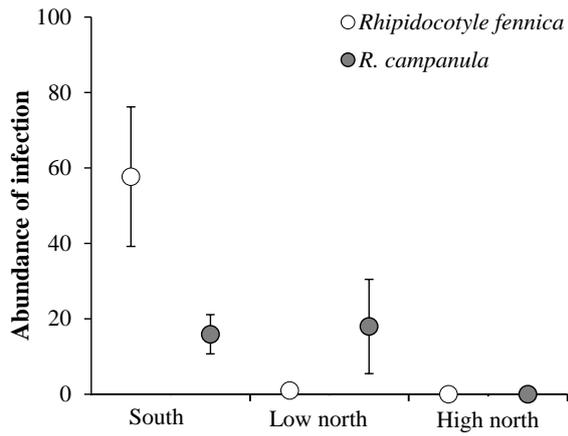
Figure 4. Average (± s.e.) site-specific mean abundance of *Rhipidocotyle fennica* and *R. campanula* infection in their second intermediate host fish, roach, in the south, low north and high north regions.