Ontogenetic dynamics of infection with *Diphyllobothrium* spp. cestodes in sympatric Arctic charr *Salvelinus alpinus* (L.) and brown trout *Salmo trutta* L.

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Abstract

The trophic niches of Arctic charr and brown trout differ when the species occur in sympatry. Their trophically transmitted parasites are expected to reflect these differences. Here, we investigate how the infections of *Diphyllobothrium dendriticum* and *Diphyllobothrium ditremum* differ between charr and trout. These tapeworms use copepods as their first intermediate hosts and fish can become infected as second intermediate hosts by consuming either infected copepods or infected fish. We examined 767 charr and 368 trout for *Diphyllobothrium* plerocercoids in a subarctic lake. The prevalence of *D. ditremum* was higher in charr (61.5 %) than in trout, (39.5 %), but the prevalence of *D. dendriticum* was higher in trout (31.2 %) than in charr (19.3 %). *Diphyllobothrium* spp. intensities were elevated in trout compared to charr, particularly for *D. dendriticum*. Large fish with massive parasite burdens were responsible for the high *Diphyllobothrium* spp. loads in trout. We hypothesize that fish prey may be the most important source for the *Diphyllobothrium* spp. infections in trout, whereas charr predominantly acquire *Diphyllobothrium* spp. by feeding on copepods. Our findings support previous suggestions, that the ability to establish in a second piscine host is greater for *D. dendriticum* than for *D. ditremum*.

Introduction

Competition between similar species can lead to niche shifts and reduced diet overlap (Harrington et al., 2009; Bolnick et al., 2010). Can this also drive differences in the loads of parasites transmitted through the food web? The use of parasites as markers to elucidate aspects of host ecology is widely recognized (Williams et al., 1992; Knudsen et al., 2004, 2008; Hechinger et al., 2007; Valtonen et al., 2010). Trophically transmitted parasites are valuable tracers of long-term patterns in foraging, and are useful indicators for niche segregation at an individual or population level (Knudsen et al., 2014). This approach is commonly applied in aquatic ecosystems to explore segregation in diet and habitat use within and between fish populations (e.g. Valtonen et al., 2010; Stutz et al., 2014). For instance, fishes that forage in the pelagic zone will often be infected with copepod-transmitted parasites, whereas predators foraging in benthic areas will have higher burdens of parasites transmitted through benthic macroinvertebrates (Knudsen et al., 2004; Stutz et al., 2014). Arctic charr (*Salvelinus alpinus* (L.); hereafter charr) and brown trout (*Salmo trutta* L.; hereafter trout) are common fishes in northern Scandinavian lakes. They have similar niches in allopatry, with both species preferring benthic prey in the littoral zone (Nilsson, 1963; Klemetsen et al., 2003a). Small and young charr may also be found in the profundal and pelagic habitats (Klemetsen et al., 2003a; Amundsen et al., 2008). Both fish species are piscivorous at large body sizes (L'Abee-Lund et al., 1992). In sympatry, trout appear to exclude charr from littoral areas during summer and autumn (Nilsson, 1963; Langeland et al., 1991). This niche segregation may be reflected in the parasite communities of these two salmonids. Knudsen et al. (2008) found that charr had more copepod-transmitted parasites than did trout, and related this to charr feeding more often on zooplankton compared to trout.

Cestodes of *Diphyllobothrium*, mainly *D. dendriticum* (Nitzsch, 1824) and *D. ditremum* (Creplin, 1825) indicate the diets of lake-dwelling charr and trout (e.g. Bérubé & Curtis, 1986; Frandsen et al., 1989; Knudsen et al., 2008). These parasites, which are transmitted to fish when they feed on copepods, become adults in piscivorous birds and, for *D. dendriticum,* some mammals (Halvorsen, 1970). Infected fish can function as paratenic hosts, so piscivorous fish can also become infected. Hence, there are two contrasting feeding pathways, zooplanktivory and piscivory, through which fish can acquire *Diphyllobothrium* species. Large fish that become piscivorous might accumulate higher numbers of trophically transmitted parasites than fish that feed solely on invertebrates (Knudsen et al., 1996; Valtonen et al., 2010; Locke et al., 2014; Münster et al., 2015). For *Diphyllobothrium* spp., fish feeding solely on zooplankton typically have low to moderate parasite intensities (< 100), whereas piscivorous individuals can accumulate hundreds or thousands of parasites (Curtis, 1984; Hammar, 2000; Gallagher & Dick, 2010). High aggregations of *Diphyllobothrium* spp. in large fish can therefore be considered an indicator of piscivorous behaviour (Gallagher & Dick, 2010).

Here, we investigate infection prevalences and intensities of *D. dendriticum* and *D. ditremum* in sympatric charr and trout. We relate the infection patterns to ontogenetic changes in the diet and habitat of the hosts. In particular, we investigate the role of zooplanktivorous versus piscivorous behaviour in relation to *Diphyllobothrium* species infections. An important difference between these two feeding strategies is that only larger charr and trout eat fishes (L’Abee-Lund et al., 1992) whereas all sizes can eat zooplankton. Parasites that do not depend on fish size for transmission should accumulate with fish age, whereas parasites that depend on a threshold fish size should be more related to fish size than age (Zelmer & Arai, 1998). Charr are often zooplanktivorous in sympatry with trout (Langeland et al., 1991), and start feeding on zooplankton at small and intermediate sizes (Klemetsen et al., 2003a, 2003b; Amundsen et al., 2008). Trout, on the other hand, are seldom zooplanktivorous, and are often piscivorous in sympatry with potential prey fishes like charr and stickleback (L’Abee-Lund et al., 2002; Klemetsen et al., 2003a; Sánchez-Hernández & Amundsen, 2015). We hypothesize that the prevalences and intensities of the *Diphyllobothrium* species will reflect the different feeding strategies of charr and trout, with charr acquiring infections through feeding on copepods while trout become infected through piscivory.

We predicted that the prevalences of *Diphyllobothrium* spp. would be higher in charr than in trout, because more of the population feeds on potential hosts (copepods and fish). Further, we predicted that the zooplanktivorous charr become infected with cestode-larvae at smaller sizes than do trout. On the other hand, we predicted that the intensities would be elevated in trout compared to charr, because piscivores accumulate more parasites. *Diphyllobothrium* spp. accumulate in intensity over the life of their hosts (Henricson, 1977; Halvorsen & Andersen, 1984). We predicted that the prevalence and intensity of cestodes in charr reflects fish age more than fish size, whereas in trout, size is more important than age. An experimental study found *D. dendriticum* to be superior to *D. ditremum* in re-establishing in a second piscine host (Halvorsen & Wissler, 1973), but the results of this study have been questioned

(Curtis, 1984). Assuming such differential re-establishment rates, we predicted a higher ratio of *D. dendriticum* to *D. ditremum* in trout compared to charr as a consequence of the contrasting transmission pathways to the two fish species.

Materials and methods

Fish were sampled in a subarctic lake, Takvatn in northern Norway (69°07´N, 19°05´E) annually between 2001 and 2011. The fish community of Takvatn consists of charr, trout and three-spined stickleback (*Gasterosteus aculeatus* L.; hereafter stickleback). For a more detailed description of the lake and its biota see Klemetsen et al. (1989). We caught 767 charr and 368 in autumn using multi-mesh gillnets set overnight in the littoral, pelagic and profundal zones of the lake. Young small-sized fish were underrepresented in the samples, as is common due to gill-net selectivity (Finstad et al., 2000). The fish were weighed (to the nearest 0.1 g), fork length measured (to the nearest 1 mm), and sex and gonad maturation status were recorded. Age determination was done by surface readings of otoliths submerged in glycerol (Klemetsen et al., 2002). Parasite sampling was conducted by placing visceral organs and fish muscle containing *Diphyllobothrium* spp. plerocercoids in digestive fluid (2 ml HCl, 5 g pepsin, 9 g NaCl, in one liter water) to excyst the parasites. The excysted parasites were preserved in 4 % buffered formalin and later counted and identified to species in the laboratory following Andersen & Gibson (1989).

Length and age distributions of the two fish populations were not normally distributed (D’Agostino-Pearson’s K2 normality test, all $P < 0.001$), and differences between the species were tested using two-sample Kolmogorov-Smirnov tests. Parasitological terms (prevalence, abundance, intensity) are according to Bush et al. (1997). All parasite analyses were conducted separately for the two *Diphyllobothrium* species. *Diphyllobothrium* prevalences were compared between charr and trout using Fisher’s exact test. We used logistic regression to investigate the relationship between the probability of infection and fish size, with uninfected and infected fish as the binomial response variable and fork length as the predictor. Potential differences between charr and trout were explored by including fish species as a variable in the analysis.

Differences in *Diphyllobothrium* intensities between charr and trout were tested using the Brunner-Munzel test, as recommended by Neuhäuser & Poulin (2004). Variance-to-mean ratios of tapeworm abundance are provided as a measure of parasite aggregation. A distribution is considered aggregated when this ratio is greater than unity (Shaw & Dobson, 1995).

To assess the relative importance of length and age on infection probability, we included both as predictors in the same logistic model with an interaction term between length and age to control for differences in growth rates. Separate models were run for each fish and parasite species combination. The importance of fish age and length for parasite intensity was explored using Spearman rank correlations.

The relative intensities of *D. dendriticum* and *D. ditremum* in fish that were infected with both parasite species were compared between charr and trout, and the effect of fish length on this ratio was tested using linear regressions.

Statistical analyses were conducted in GraphPad Prism 6 for mac and with R (v. 3.1.0. R Development Core Team, 2014).

Results

Charr and trout demography

Charr averaged 198 mm in length (range 84 – 474) and 4.6 years in age (range 2 – 14), and trout averaged 238 mm in length (range 70 – 634) and 4.1 years in age (range 1 – 11) (Fig. 1). Length and age distributions did not differ significantly between charr and trout (length, D = 0.3000, p = 0.1344; age, D = 0.1429, p = 0.9988).

Prevalence of *Diphyllobothrium* species

The prevalence of *D. ditremum* was higher in charr than trout ($P < 0.001$), with more than 60 % of the charr being infected (Table 1). For *D. dendriticum*, the prevalence was lower compared to *D. ditremum* in both fish species (Table 1), and more trout than charr were infected ($P < 0.001$). The two parasite species also displayed different patterns in the infection probability with increasing fish length (Fig. 2). Charr became infected with *D. ditremum* at significantly smaller sizes than did trout ($P = 0.028$). Fifty percent of charr were infected with *D. ditremum* at a length of 161 mm, whereas trout reached 50 % prevalence at 261 mm (Fig. 2a). An opposite pattern was observed for *D. dendriticum*, where trout became infected at smaller sizes than did charr ($P = 0.047$). Trout reached 50 % prevalence at 296 mm, charr at 354 mm (Fig. 2b).

Intensity of *Diphyllobothrium* species infections

The mean intensity of *D. ditremum* was slightly higher in trout than in charr (Table 1), but this difference was not significant ($P = 0.352$). In contrast, the mean intensity of *D. dendriticum* differed greatly between the two fish species, with intensities being far higher in trout (Table 1, $P < 0.001$). Parasite distributions were more aggregated in trout, particularly for *D. dendriticum,* as evidenced by the variance-to-mean ratios (Table 1). It seems this aggregation stems from a few large trout with high parasite burdens (Fig. 3). The mean intensity of both *Diphyllobothrium* species increased exponentially with increasing size in trout, and the two largest size groups of trout had far higher infections than did smaller trout (< 350 mm, Fig. 3). In contrast, the mean intensity of both parasite species in charr reached an asymptote at around 250 mm fish length (Fig. 3).

Effects of length and age on parasite abundance

Both length and age influenced the probability of infection for the two *Diphyllobothrium* species in charr, whereas only length was important in trout (Table 2). The intensities of the two *Diphyllobothrium* species were positively correlated with fish age and length for both charr and trout (Table 3). Correlations were higher for *D. ditremum* compared to *D. dendriticum* in charr, but the opposite pattern was observed for trout (Table 3). Age and length were equally important predictors for parasite intensities for charr, whereas, for trout, parasite intensities were more correlated to length than with age.

Ratios of *D. dendriticum* to *D. ditremum*

In fish infected with both parasite species the ratio of *D. dendriticum to D. ditremum* was greater in trout than in charr (Fig. 4), the relative intensity of *D. dendriticum* being higher in trout. There was a decline in this ratio with increasing fish length for charr ($P = 0.0268$), whereas the ratio increased strongly with trout size ($P < 0.001$) (Fig. 4).

Discussion

Based on general dietary niches of charr and trout in sympatry (Nilsson, 1963; Langeland et al., 1991; Knudsen et al., 2008; Eloranta et al., 2013), we expected the transmission routes and the resulting infection patterns of two *Diphyllobothrium* species to differ between the fish species. The observed differences in *Diphyllobothrium* infections largely confirmed the expected copepod transmission route in charr, and the piscivorous transmission route in trout. Our results are further supported by earlier dietary analyses and food web studies at Takvatn that have confirmed the resource partitioning between charr and trout, with zooplanktivory in charr and piscivory in trout (Amundsen & Klemetsen, 1988; Knudsen et al., 1996; Klemetsen et al., 2002, 2003b; Amundsen et al., 2009). The stability and coexistence of the two species in Takvatn, may be facilitated through trout predation on small charr (Persson et al., 2007, 2013).

Diphyllobothrium species infection patterns in charr seem to be based on copepod transmission. Because zooplanktivory is common in small charr (Klemetsen et al., 2003a, 2003b; Amundsen et al., 2008), and piscivory is restricted to larger fish (L'Abee-Lund et al., 1992; Amundsen, 1994), a larger proportion of the charr population should be susceptible for infection compared to trout. In accordance with our prediction, the prevalence of *D. ditremum* was higher in charr than trout. Charr also became infected with the parasite at small lengths that correspond to the pelagic and zooplanktivorous phase of their ontogeny (L'Abée-Lund et al., 1993; Amundsen et al., 2008). Tapeworm intensities levelled off in charr larger than 250 mm, suggesting that large charr in Takvatn do not become primarily piscivorous. Such an asymptote could also be due to acquired immunity in larger charr (Woolhouse, 1998). However, the cellular immune responses to *Diphyllobothrium* plerocercoids seem to be poorly developed in salmonids (Bylund, 1972; Sharp et al., 1992). Another hypothesis is differential mortality of heavily infected fish. However, the charr population of Takvatn previously had much higher *Diphyllobothrium* species intensities without apparent mortality (Kristoffersen, 1993; Knudsen & Klemetsen, 1994). We suggest that the asymptote in *Diphyllobotrhium* species intensities with increasing fish size is related to large charr switching to feeding on benthic invertebrates that are not hosts for *Diphyllobothrium* spp.. This is supported by dietary analyses from Takvatn charr, where charr above 200 mm fed more on amphipods and molluscs, and less on zooplankton than did smaller charr (< 200 mm) (Klemetsen et al., 2003b).

The low prevalence of *D. dendriticum* in charr, and the large size for charr to become infected did not support our predictions. This could be due to piscivory in the charr at Takvatn (Amundsen, 1994; Knudsen et al., 1996). However, the intensities of *D. dendriticum* were low in the charr population throughout their ontogeny. The lower abundance of *D. dendriticum* compared to *D. ditremum* appears to be a recurring pattern in northern areas (e.g. Henricson, 1977; Knudsen et al., 2004). It is also consistent with the findings of a parasitological study of the stickleback population of Takvatn (Kuhn et al., 2015), where 773 *D. ditremum* individuals were found, but only one *D. dendriticum*. Thus, the long time it took for charr to become infected with *D. dendriticum* probably reflects the scarcity of the parasite in the system rather than a piscivorous diet, because there were low infection levels in even the large charr.

The majority of the trout population was uninfected with *Diphyllobothrium* spp., but the intensities of particularly *D. dendriticum*, were elevated in trout compared to charr as predicted based on potential piscivorous transmission. *Diphyllobothrium* species were more aggregated in trout with many larval specimens in the largest fish. Increasing amounts of evidence suggest that trophic level can structure parasite communities in fish (Poulin & Valtonen, 2001; Marcogliese, 2002; Timi et al., 2011, Strona & Lafferty, 2013), and higher aggregations of trophically transmitted parasites can be the result of a higher position in the trophic chain (Lester, 2012). Shifts in trophic level during the ontogeny of a fish should, therefore, be followed by an increase in trophically transmitted parasites. In Greenland cod, for instance, infections with anisakid nematodes were indicative of an ontogenetic switch to piscivory (Münster et al., 2015). Similarly, *Diphyllobothrium* spp. infections were used to explore the trophic structure and extent of piscivory in a population of Arctic charr (Gallagher & Dick, 2010). The exponential increase in *Diphyllobothrium* intensities in large trout from Takvatn therefore reflects the switch to feeding at a higher trophic level, i.e. the inclusion of sticklebacks and charr in the diet (Persson et al., 2007; Amundsen et al., 2009).

Both *Diphyllobothrium* species in this study are important components of the pelagic food web in Takvatn (Amundsen et al., 2009). The piscivorous habit of trout results in many *Diphyllobothrium* individuals ending up in a few large trout. 63.1 % of *D. ditremum* specimens and 82.3 % of *D. dendriticum* specimens infecting trout were found in fish larger than 350 mm. Unless large carcasses are scavenged or fish entrails are discarded by fishermen where other hosts can eat them, these fish are likely too large for birds (Amundsen et al., 2009) to prey on, and therefore could represent a dead-end in the life cycles of these tapeworms. Importantly, this parasite population sink may significantly affect the transmission dynamics of the two parasite species in the system.

As predicted, size was the most important explanatory factor for *Diphyllobothrium* spp. infections in trout, whereas the effects of size and age were similar in charr infections. Body size increases with the age of fish, so typically the elevated parasite burdens found in large fish reflect the longer time these fish have been exposed to parasites (Pacala & Dobson, 1988; Zelmer & Arai, 1998; Poulin, 2000). Thus, long-lived fish parasites that reside in intermediate hosts whose ingestion is not limited by fish size should accumulate with both fish age and size. This was the observed pattern in charr from Takvatn. However, as pointed out by Zelmer & Arai (1998), parasites that reside in intermediate hosts whose ingestion is limited by fish size should accumulate as an effect of fish length rather than age. This appears to be the case for trout in the present study. Transmission of *Diphyllobothrium* spp. to trout may be dependent on a threshold size, thus reflecting piscivory in the larger fishes.

The higher ratio of *D. dendriticum* to *D. ditremum* in trout compared to charr is also indicative of piscivorous feeding in trout, because *D. dendriticum* have been found to be superior to *D. ditremum* when re-establishing in paratenic fish hosts (Halvorsen & Wissler, 1973). Considering the low number of *D. dendriticum* in potential prey fishes, small charr and sticklebacks in Takvatn (Kuhn et al., 2015; present study), our results provide support for the hypothesis that *D. dendriticum* is better than *D. ditremum* at re-establishment in a second fish host. Both sticklebacks and charr are important prey items for the Takvatn trout (Amundsen et al., 2009). The relative increase of *D. dendriticum* with trout size suggests that larger trout include more charr in their diet, because charr at Takvatn appear to be more infected with the parasite than are sticklebacks (Kuhn et al., 2015; present study). This could, however, also be due to interspecific interactions between the two parasite species, where *D. dendriticum* prevents successful colonization of *D. ditremum*, as suggested by Kristoffersen (1993).

Here, we assumed that charr and trout have equal susceptibility to *Diphyllobothrium dendriticum* and *D. ditremun* infections. However the observed differences could also be due to charr having a lower susceptibility to infection by *D. dendriticum* than *D. ditremum*. In an experimental study, 62.5 % of charr exposed to larval *D. dendriticum* became infected (Blanar et al., 2005), which is similar to transmission studies done with trout (53.2 %) (Halvorsen, 1970). In general, the host specificity of the *Diphyllobothrium* genus seems to be low (Vik, 1964; Halvorsen, 1970)**.** Differences in susceptibility to *Diphyllothrium* spp. are nevertheless an unknown factor that requires further study.

Overall, our results support the hypothesis that charr become infected with most *Diphyllobothrium* spp. through copepod feeding, while trout acquire these parasites as paratenic hosts through piscivory. When trout are present, charr are restricted to a more pelagic habitat and diet (Eloranta et al., 2013). This likely reduces their access to piscivory, and could result in a lower parasite burden in charr. In contrast to the low level of *Diphyllobothrium* spp. infections we observed in charr from Takvatn, charr residing in lakes without any trout feed on small prey fishes or were cannibalistic at larger sizes. This results in the presence of thousands of

Diphyllobothrium plerocercoids due to paratenesis (Hammar, 2000; Gallagher & Dick, 2010). Under a sympatric charr-trout scenario as in Takvatn, competition likely leads to a habitat and diet change that alters exposure to parasites. In this respect, the displacement of subordinate charr from the littoral feeding grounds by trout (Langeland et al., 1991; Eloranta et al., 2013), while reducing food quality, appears simultaneously to reduce the risk of parasitism when charr are restricted from the piscivorous niche. This is supported by earlier Takvatn studies showing charr to be piscivorous (Amundsen, 1994; Knudsen et al., 1996) when the trout population was low (Klemetsen et al., 2002; Persson et al., 2007). Hence, the parasite burden in these lacustrine ecosystems may be governed by interspecific and intraspecific (extent of cannibalism) host behavioral interactions.

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Tables

Table 1 Infections of *Diphyllobothrium* sp. in Arctic charr (n = 767) and brown trout (n = 368) in Takvatn. Values for P = prevalence, MA = mean abundance, MI = mean intensity and variance-to-mean ratio (abundance) are shown. Standard errors in parentheses.

	Diphyllobothrium ditremum				*Diphyllobothrium dendriticum*			
	P	MA	MI	Var/x̄	P	MA	MI	Var/x̄
Arctic charr	61.5 %	6.70 (0.52)	10.89 (0.78)	30.76	19.3 %	0.57 (0.09)	2.95 (0.43)	11.57
Brown trout	39.5 %	5.26 (1.14)	13.45 (2.75)	90.16	31.3 %	7.82 (2.02)	25.02 (6.17)	192.84

Table 2 Statistical results (log odds) from logistic regressions of probability of infection (uninfected or infected) versus fish length, fish age and their interaction for *D. dendriticum* and *D. ditremum* in Arctic charr and brown trout in Takvatn. Significance levels are given (P; * < 0.05, ** < 0.01, *** < 0.001).

	D. dendriticum		*D. ditremum*	
	Arctic charr	brown trout	Arctic charr	brown trout
Intercept	– 7.600 ***	– 4.656 ***	– 5.701 ***	– 5.142 ***
Length	0.026 ***	0.021 ***	0.023 ***	0.026 ***
Age	0.773 ***	– 0.197	0.988 ***	– 0.080
Length:Age	– 0.003 ***	– 0.000	– 0.003 ***	– 0.001

Table 3 Spearman rank correlations between parasite intensity and fish age and length for Arctic charr and brown trout in Takvatn. Parentheses indicate 95 % confidence levels. Significance levels are given (P; * < 0.05, ** < 0.01, *** < 0.001).

	D. dendriticum	*D. ditremum*
Arctic charr age	0.27 (0.11–0.42) **	0.50 (0.42–0.57) ***
Arctic charr length	0.27 (0.10–0.41) **	0.48 (0.41–0.55) ***
Brown trout age	0.27 (0.08–0.45) *	0.17 (0.00–0.34) *
Brown trout length	0.47 (0.31–0.61) ***	0.30 (0.14–0.45) ***

Legends

Fig. 1 Age (a) and length (b) distributions of Arctic charr (black bars) and brown trout (grey bars) sampled for parasitological investigation between 2001 and 2011 from Takvatn.

Fig. 2 Logistic regressions showing the probability of being infected with increasing fish length for *D. ditremum* (a) and *D. dendriticum* (b) in Arctic charr (dashed line) and brown trout (solid line) from Takvatn.

Fig. 3 Mean intensity (± standard error) of *D. ditremum* (a, b) and *D. dendriticum* (c, d) for different length groups of Arctic charr (a, c) and brown trout (b, d) from Takvatn. Number of fish in each length group is shown on top of the graph. Note the difference in y-axis scale for *D. dendriticum*.

Fig. 4 Linear regressions (solid lines) between fish length and the ratio of *Diphyllobothrium dendriticum* to *D. ditremum* in Arctic charr (a, slope = – 0.0012, $r^2 = 0.03$, $P = 0.0268$) and brown trout (b, slope = 0.0017, $r^2 = 0.14$, $P < 0.0001$) from Takvatn. The stippled lines indicate equal numbers of the two parasite species. Note the difference in scale on the y-axis for the two fish species.

Fig 1

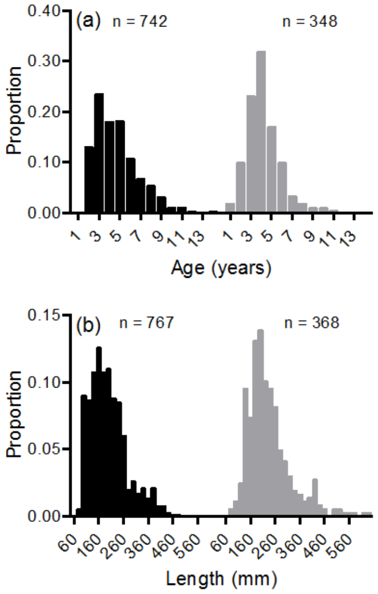

(a)
n = 742
n = 348
Proportion
0.40
0.30
0.20
0.10
0.00
1 3 5 7 9 11 13 1 3 5 7 9 11 13
Age (years)
(b)
n = 767
n = 368
Proportion
0.15
0.10
0.05
0.00
60 160 260 360 460 560 60 160 260 360 460 560
Length (mm)

Fig 2

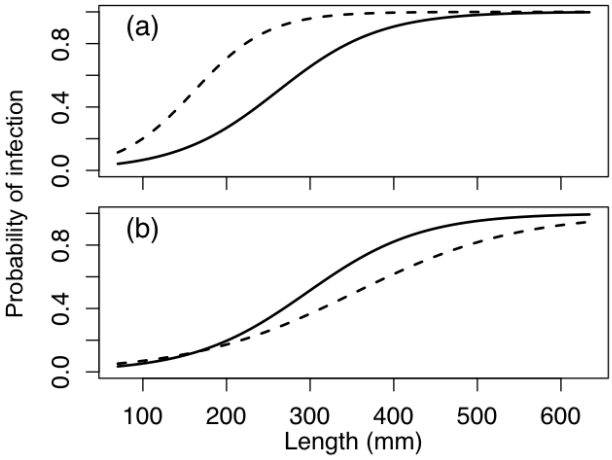

(a)
(b)
Probability of infection
0.0
0.4
0.8
0.0
0.4
0.8
100
200
300
400
500
600
Length (mm)

Fig 3

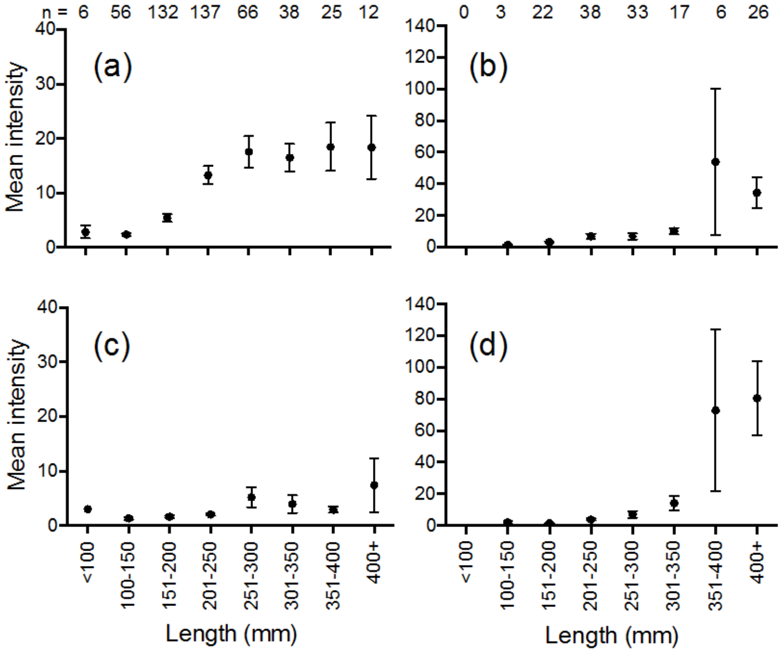
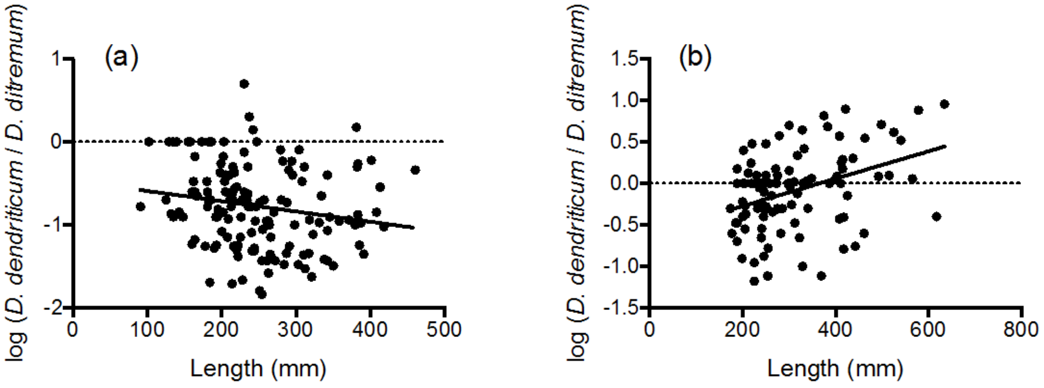

n = 6 56 132 137 66 38 25 12
0 3 22 38 33 17 6 26
(a)
(b)
(c)
(d)
Mean intensity
Mean intensity
0
10
20
30
40
0
20
40
60
80
100
120
140
<100
100-150
151-200
201-250
251-300
301-350
351-400
400+
Length (mm)
Length (mm)

Fig 4


(a)
log (*D. dendriticum* / *D. ditremum*)
1
0
-1
-2
0
100
200
300
400
500
Length (mm)
(b)
log (*D. dendriticum* / *D. ditremum*)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
200
400
600
800
Length (mm)