Cestode infection in a polymorphic whitefish population

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Running title: Cestodes in polymorphic whitefish

Abstract

The whitefish (*Coregonus lavaretus* s.l.), stock in Lake Femunden, Norway, includes three morphs: D-, R- and S-whitefish. Infections by *Diphyllobothrium* spp. and *Triaenophorus crassus* in the morphs were monitored during 1988-2005. In all three morphs *T. crassus* prevalence increased significantly, but at a varying rate, with age. In juvenile fish, prevalence was lowest in D-whitefish and highest in S-whitefish. As the rate of increase was lower in R- and S-whitefish than in D-whitefish, prevalence was more equal in older fish. The relative differences in parasite load of *T. crassus* among the three whitefish morphs appear mainly to be in line with the morph differences in habitat use, and associated with the habitat use of the final host of the parasite (pike, *Esox lucius*).

Almost all individuals of D-, R- and S-whitefish were infected by *Diphyllobothrium* spp., with prevalence higher than 75% from age 2. In all three whitefish morphs, mean abundance of *Diphyllobothrium* spp. increased with the age of the fish, with the most rapid increase in young age groups. The development of infection with age was almost identical in S- and D-whitefish, whereas R-whitefish was at a higher level from an early age. The high prevalence of *Diphyllobothrium* spp in all three whitefish morphs probably reflects the distribution of parasite eggs over all lake habitats by the avian final hosts. The differences in the mean abundance of *Diphyllobothrium* spp. with age, with a heavier parasite load in R-whitefish than the nearly identical levels in D- and S-whitefish, is not easily explained by differences in habitat use or diet among the whitefish morphs.

Keywords: parasite load, polymorphism, habitat use, parasite abundance, parasite intensity, prevalence

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Introduction

Whitefish (*Coregonus lavaretus s.l.*) is a common intermediate host of the cestodes *Diphyllobothrium ditremum, D. dentriticum* and *Triaenophorus crassus* in boreal lakes (Watson, 1979; Amundsen, 1988; Pulkkinen & Valtonen, 1999, Tolonen et al. 2000). In Europe, the final host of *T. crassus* is the piscivorous Northern pike (*Esox lucius*), while the final hosts of *Diphyllobothrium* spp. are fish-eating waterbirds (e.g. gulls and mergansers) (Halvorsen, 1970). The adult parasites live in the intestines of the final host, and the cestode eggs are released with the faeces. The free swimming coracidium larvae hatch from the eggs and are ingested by copepods, in particular of the genus *Cyclops* (Pasternak et al., 1995; 1999; Pulkkinen et al., 2000). The fish are infected when preying on copepods. Thus, it should be expected that the parasite load of the whitefish through its life cycle is related to the habitat use of the final hosts and the first intermediate hosts (copepods), as well as the ontogenetic niche shifts (habitat use and diet) of the whitefish (Sandlund et al., 1995).

Whitefish commonly occur in polymorphic populations; the morphs have different ecologies, including habitat use, diet and spawning location (e.g. Kahilainen et al., 2007; Siwertsson et al., 2010). This is also the case for the three whitefish morphs in Lake Femunden (Sandlund et al., 1995; Næsje et al., 1998; Saksgård et al., 2002). These ecological differences may entail different risks of becoming infected by trophically transmitted parasites, and consequently on the relative parasite load of the whitefish morphs (Knudsen et al., 2003; Karvonen et al., 2013).

The plerocercoids of *T. crassus*, which develop in the sceletal muscle tissue of the fish which is the second intermediate host, is large relative to host size, and *T. crassus* infection is known to affect fish growth negatively (Miller, 1945; Pulkkinen & Valtonen, 1999). As the plerocercoids have a life span of several years, one would expect that infection levels should increase with fish age (Amundsen & Kristoffersen, 1990; Pulkkinen & Valtonen, 1999). Infection by *T. crassus* may render the whitefish unsuitable for consumption. The plerocercoids of *Diphyllobothrium* spp. are found encysted on the stomach wall, in the viscera and sometimes in the muscle of the second intermediate host, which may also be a paratenic host as infected fish may be eaten by piscivorous fish. The prevalence and intensity of *Diphyllobothrium* spp. plerocercoids have been shown to increase with fish age (Tolonen et al., 2000). At high infection rates *D. dentriticum* may migrate to other internal organs of the fish, possibly causing the death of the host (Rahkonen et al., 1996). *D. ditremum* migrates less within its host, and is considered to have little effect on fish condition and survival (Halvorsen 1970). At low to moderate infection levels, *Diphyllobothrium* does not affect the quality of fish for consumption.

The aim of this paper is to analyze the relative parasite infection load through life in three whitefish morphs in a natural lake system little influenced by human activities. During the monitoring of the polymorphic whitefish population in Lake Femunden from 1988 to 2005, the prevalence and intensity of *T. crassus* and *Diphyllobothrium* spp. were recorded.

Material and methods

Lake Femunden (662 m a.s.l., 62° 0' N 11° 55' E) is the second largest natural lake in Norway with a surface area of 204 km² and a maximum and mean depth of 134 m and 30 m, respectively. The lake is ultraoligotrophic, and is the uppermost major lake in the catchment area of River Klarälven, which

drains towards the southeast into Lake Vänern in Sweden. Sandlund & Næsje (1989) and Sandlund et al. (2004) provide more detailed information about the lake.

The whitefish population in Lake Femunden was studied by Svärdson (1979). Based on gillraker numbers he differentiated between three forms. Gillraker distribution from survey and commercial net catches has confirmed his observation of a trimodal distribution, and for management purposes three forms of whitefish (called morphs in this paper) have been defined (Sandlund & Næsje, 1989). These are deepwater (D-) whitefish, river (R-) whitefish and shallow water (S-) whitefish (table 1). The morphs differ clearly by length and age at sexual maturity (Næsje et al., 1998), and they differ genetically (Næsje et al., 2004). For this paper, we maintain the three forms of whitefish based on gillraker number, although a closer examination based on microsatellites and morphometry has identified an additional, but scarce, fourth genetic group of whitefish in Lake Femunden (Østbye et al., 2005).

There are eight fish species in Lake Femunden; in addition to whitefish these are: northern pike (*Esox lucius* L.), Arctic charr (*Salvelinus alpinus* (L.)), brown trout (*Salmo trutta* L.), grayling (*Thymallus thymallus* (L.)), perch (*Perca fluviatilis* L.), burbot (*Lota lota* (L.)), and minnow (*Phoxinus phoxinus* (L.)). There have been no introductions of non-native fish species into the lake. A commercial whitefish fishery was initiated in 1981 (Sandlund & Næsje, 1996; Sandlund et al., 2004). The occurrence of *Triaenophorus crassus* and *Diphyllobothrium* spp. were recorded in all whitefish sampled from the annual commercial catches from 1988 to 2005, and from gill net surveys in 1990, 1991, 1994 and 1999.

A routine set of samples were taken from the fish (Sandlund & Næsje, 1989; Saksgård et al., 2002; Ugedal et al., 2002). In this paper, we report data for age and gillraker counts in addition to parasite counts. Fish were aged from otoliths, which were burned, broken, and read under a stereo microscope (cf. Skurdal et al., 1985). Gillrakers were counted on the anterior left gill arch. An index for the presence of *T. crassus* plerocercoids were obtained by cutting two transversal cuts through the dorsal muscle mass (one between the head and the dorsal fin and one immediately behind the dorsal fin), and counting the number of plerocercoids visible on the two cuts. This provides minimum values for the occurrence of the parasite (i.e. prevalence). This sampling strategy provides relatively low values for the number of detected parasites (0-4 plerocercoids per fish). The plerocercoids of *Diphyllobothrium* were recorded by counting the number of cysts on the wall of the oesophagus and stomach of the fish. The actual number of cysts was noted for up to 25 cysts, while the occasional higher number also was noted as 25 cysts. We did not distinguish between the two species of *Diphyllobothrium* recorded in salmonids in this area (*D. ditremum* and *D. dendriticum*).

Data on parasite infection were recorded for altogether 8872 fish (5352 D-whitefish, 2924 R-whitefish and 596 S-whitefish).

When modeling prevalence, we fitted a generalized linear mixed model (GLMM) with a binomial error distribution, logit as link function, and year as a random factor (e.g. McCulloch & Searle, 2001). Fixed factors included in the full model were fish age, morph (D-, R- or S-whitefish) and the interaction term age:morph. The *glmer* function from the R package *lme4* was used to fit the generalized linear mixed models (R core team, 2017). In modelling the number of *Diphyllobothrium* cysts per fish vs. age in three whitefish morphs, fish without parasites had to be included due to the

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assumption of a Poisson distributed response variable. Thus we were modelling mean abundance (mean number of parasites in all examined fish) rather than mean intensity (mean number of parasites in infected fish). A GLMM was fitted to the parasite abundances with a Poisson error distribution, the natural logarithm as link function, and year as a random factor. Fixed factors included in the full model were fish age, morph (D-, R- or S-whitefish) and the interaction term age:morph. To check if we needed to control for over-dispersion in this model, i.e. if the error distribution has a variance larger than the model expects, a generalized linear model with a quasi-poisson error distribution was fitted.

Results

Triaenophorus crassus

Our sampling strategy for *T. crassus* provided low values for infection intensity (0-4 plerocercoids per fish). Although infection intensity varied over the sampling period from 1988 to 2005, there was no significant trend over the years. Neither was infection intensity different among whitefish morphs. The mean annual values for infection intensity ± SD were: D-whitefish: 1.77 ± 1.29; R-whitefish: 1.64 ± 0.97; and S-whitefish: 1.72 ± 1.18.

The prevalence of *T. crassus* did differ significantly among the whitefish morphs. All variables (age, morph and the interaction between morph and age) gave a significant contribution to the GLMM model for prevalence (table 2), where the intercept corresponds to D-whitefish with age zero. *T. crassus* prevalence increased significantly with age in all three morphs, but the rate of increase was lower in R- and S-whitefish than in D-whitefish. The difference in prevalence of *T. crassus* was particularly obvious among juvenile fish (figure 1). In S-whitefish, prevalence (expressed as percent) was 27% already at age 4, with a mean prevalence for age 2-4 at 23.7 %. R-whitefish appeared to be infected at a slower rate, with a prevalence 19% at age 4, and a mean value for age 2-4 at 10.7%. D-whitefish was infected even slower, with a mean prevalence in age groups 2-4 at 3.7%, and prevalence remaining below 10% up to an age of 6 years.

The model for prevalence (table 2) shows a significant positive effect of age ($P < 0.001$), and significant differences between the morphs. The gradients for the logit-linear model were not significantly different for the D- and R-morphs ($P = 0.156$ for *Age:R-whitefish*) while the S-morph had a slower increase in prevalence with age ($P = 0.012$) (figure 1, colored lines). From the age of 5 years, the rate of increase in prevalence with age was rapid in D-whitefish, somewhat slower in R-whitefish, and slowest in S-whitefish. In fish older than 15 years, the prevalence of *T. crassus* appeared quite similar in all three morphs. It should be noted that the number of S-whitefish is low in age groups older than 15 years.

Diphyllobothrium spp.

Almost all sampled whitefish in Lake Femunden were infected by *Diphyllobothrium* spp. In the total material, prevalence was 95% in D-whitefish, 98% in R-whitefish 94% in S-whitefish. Prevalence was lower in young fish, but reached >75% already at age 2 in all three morphs (figure 2), with no difference among the morphs.

The model for abundances of *Diphyllobothrium* spp. from age and morph is presented in table 3. The residual deviance was larger than expected, so we had to account for over-dispersion by fitting a

GLM model with a quasi-poisson error distribution. Note that the coefficients in the model here describe the linear model for the natural logarithms of abundances. In all three whitefish morphs, mean abundance of *Diphyllobothrium* spp. increased with the age of the fish (*P<0.001*), with the most rapid increase in young age groups, as demonstrated when the ln(abundances) expected by the model is back-transformed (colored lines in figure 3). The model indicates that the development of infection with age was almost identical in S- and D-whitefish (*P=0.702*), whereas R-whitefish was at a higher level from an early age (*P<0.001*).

In D-whitefish, infection intensity (i.e. number of cysts per infected fish) appeared to stabilize from an age of 2 years, with only a small increase from a mean of 9.2 cysts in age groups 2-4, 9.6 cysts in age groups 8-10, to 12.3 cysts in age groups 15-17. In juvenile R-whitefish, infection intensity was similar to D-whitefish, with a mean number of 8.6 cysts in age groups 2-4. In older R-whitefish, however, infection intensity continued to increase, with 14.9 cysts in age groups 8-10 and 15.7 cysts in age groups 15-17. In S-whitefish, the mean intensity for the corresponding age groups was 5.2, 11.1 and 13.4, respectively.

Discussion

To be able to study a large number of fish we have used simplified methods for recording the presence of the cestodes *T. crassus* and *Diphyllobotrium* spp. in whitefish (cf. Hoffman 1999, Kuhn et al. 2017). This has facilitated the collection of several years of data within a monitoring programme with restricted resources, but the data recorded are minimum values both for prevalence, infection intensity and abundance. Kuhn et al. (2017) demonstrated that counting cysts of *Diphyllobothrium* spp. on the stomach, viscera and on the walls of the body cavity, in the same way as we have done, provided a reliable estimate of prevalence, intensity and abundance of the parasite. The occurrence of *T. crassus* has previously been recorded by various time consuming and labour intensive approaches to examine the dorsal muscle mass (Pulkkinen & Valtonen, 1999; Amundsen et al., 2002). Our approach is simpler and quicker, and with the high number of samples we suggest that it provides a useful index for prevalence for comparing parasite load in the three whitefish morphs studied.

The prevalence of *T. crassus* increased with age in all three morphs. The difference between morphs was largest in young fish, with the lowest prevalence in D-whitefish and the highest prevalence in S-whitefish. The rate of increase with age was lowest in S-whitefish, while prevalence increased at a higher, but similar, rate in D- and R-whitefish. Pike, the final host of *T. crassus*, is a species very much associated with the littoral habitat for most of its life cycle, and spawning occurs in shallow waters just after ice-off in early spring (cf. Craig, 1996). The eggs of the cestode are released prior to or during pike spawning, and the coracidia larvae hatch after a few weeks (Kuperman, 1981). The coracidia are preyed upon by late copepodit or adult stages of copepods, commonly *Cyclops* species (e.g. Pasternak et al., 1999), which subsequently are eaten by whitefish. This chain of infection mainly occurs during a few weeks in late spring and early summer (Pulkkinen et al., 2000; Lahnsteiner et al., 2009; Sichrowsky et al., 2013).

In Lake Femunden, pike spawns immediately after ice-off, and *Cyclops scutifer* is the dominant copepod species, found in high densities in the littoral as well as the pelagic habitat during early

summer (Lyche Solheim et al., 2017; T. Jensen, NINA, pers. comm.). Thus, the main body of copepods infected by *T. crassus* will likely be present in the littoral zone in early summer. S-whitefish is the morph most associated with the littoral zone. It spawns in shallow waters. The eggs hatch in early spring, and the fry, juveniles and adults seem to remain in the littoral habitat. Although we have not investigated the diet of whitefish fry (<7 cm) in Lake Femunden, it is likely that *C. scutifer* is a major component of the diet in early summer (cf. Næsje et al., 1986b). Zooplankton continues to be a major component of the diet of all sizes of S-whitefish in the littoral zone (Sandlund et al., 1995). Thus, the habitat use of pike and *C. scutifer,* and the habitat and diet of S-whitefish, is likely the reason for the very high prevalence of *T. crassus* in S-whitefish. S-whitefish had the highest growth rate and reached the largest body size of the three whitefish morphs, reaching approx. 32 cm at 4 years of age (Næsje et al., 1998). A high juvenile growth rate reflects high food consumption, likely associated with relatively high temperatures in the littoral zone. This may indicate that S-whitefish ingests a relatively high number of parasite-infected copepods during early summer, reaching a high prevalence at an early age. As the fish grows larger, the rate of increase in *T. crassus* prevalence was low. This may indicate that the large fish eat larger prey such as zoobenthos, although analysis of stomach contents indicates that littoral zooplankton is important in the diet also of larger S-whitefish (Sandlund et al., 1995).

R-whitefish mainly spawn in inlet rivers. We do not know when the hatchlings or fry migrate downstream into the lake, but in other river spawning whitefish, the downstream drift occur immediately after hatching (Næsje et al., 1986). For the young of the year R-whitefish to become exposed to the parasite, the timing of their entering the littoral zone has to match the presence of infected copepods. From a body length of approx. 7 cm, R-whitefish appear to feed almost only on zooplankton, but reaching 20 cm, larger prey becomes more important (Sandlund et al., 1995). The restricted knowledge we have on the habitat use and diet of R-whitefish might indicate that the juvenile fish would experience a similar exposure to infected *C. scutifer* as S-whitefish. However, R-whitefish has a lower juvenile growth rate, reaching approx. 26 cm at age 4 (Næsje et al., 1998). This may reflect a lower food intake, also of infected copepods, and thereby lower exposure to the parasite. This may result in a lower prevalence than in S-whitefish. In older R-whitefish, *T. crassus* prevalence increased at a faster rate than in S-whitefish. However, to fully understand the interaction between infected copepods and the various size groups of whitefish, we would need to sample on a fine temporal and spatial scale in the lake.

D-whitefish spawns in deep waters (>30 m). The juveniles appear to stay in relatively deep and cold waters (>10 m), with a low growth rate until they reach approx. 20 cm in length (4-6 years) (Næsje et al., 1998). Larger D-whitefish to a large extent utilize pelagic waters (Saksgård et al., 2002). Thus, the overlap between D-whitefish and *C. scutifer* infected by *T. crassus* may appear to be low (Sandlund et al., 1995).

Whitefish is infected by *Diphyllobothrium* spp. in the same way as by *T. crassus*, i.e. by ingesting infected cyclopoid copepods (Vik, 1964). However, in this case the cestode eggs reach the water in the faeces of fish eating birds. Although gulls and mergansers likely feed mainly in shallow waters, they will be flying across the lake surface in all directions, contributing to more or less indiscriminate spreading of *Diphyllobothrium* eggs over the entire lake surface. Upon hatching, the coracidia larvae may infect copepods in all lake areas. This is probably one reason that prevalence is close to 100% in all three whitefish morphs already from a young age. Similar high prevalence of *Diphyllobothrium*

spp. in whitefish have also been observed in other studies (Tolonen et al., 2000; Knudsen et al., 2003).

The difference between whitefish morphs in terms of parasite load expressed as mean abundance vs. age is difficult to explain. Infection intensity increased with age in all three morphs. However, the abundance models for D- and S-whitefish were almost identical, while R-whitefish was at a significantly higher level in all age classes.

Any explanation for this discrepancy must be speculative. The most numerous R-whitefish stock spawn in the Tufsinga River, which empties into Lake Femunden through a delta area, which is a nature reserve and Ramsar site partly established to protect water birds (Tufsinga Delta, http://faktaark.naturbase.no/Vern?id=VV00001867). It may be speculated that the fry and juveniles spend time in the delta area together with a high density of birds (gulls and mergansers), whose droppings may cause a high infection of *Cyclops* by *Diphyllobothrium* coracidia. However, the Tufsinga delta is also one of the major spawning areas for pike in Lake Femunden. This should also lead to a high exposure of R-whitefish to infection by *T. crassus*.

In summary, the pattern of parasite load in the three whitefish morphs in Lake Femunden differ between T. crassus and *Diphyllobothrium* spp. For *T. crassus,* the relative differences in parasite load of among the three whitefish morphs appear largely to be in line with the differences in habitat use among the whitefish morphs in relation to the habitat use of the final host, northern pike. On the other hand, the high prevalence of *Diphyllobothrium* spp. in all three whitefish morphs probably reflects the distribution of parasite eggs over all lake habitats by the avian final hosts. The differences in the mean abundance of *Diphyllobothrium* spp. with age, with a heavier parasite load in R-whitefish than the nearly identical levels in D- and S-whitefish, is puzzling.

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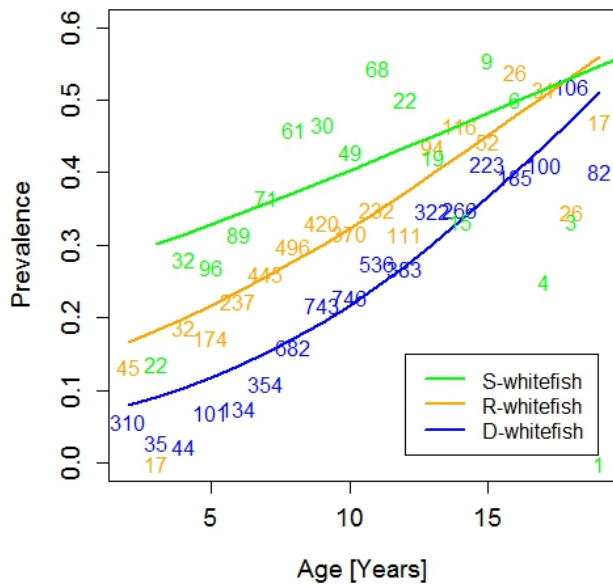
Figure 1. Illustration of the relationships between fish age (x) and prevalence of *T. crassus* (y) in three whitefish morphs (S-, R- and D-whitefish) in Lake Femunden. N is number of fish analyzed per age group and whitefish morph. Note the narrower age span in S-whitefish.
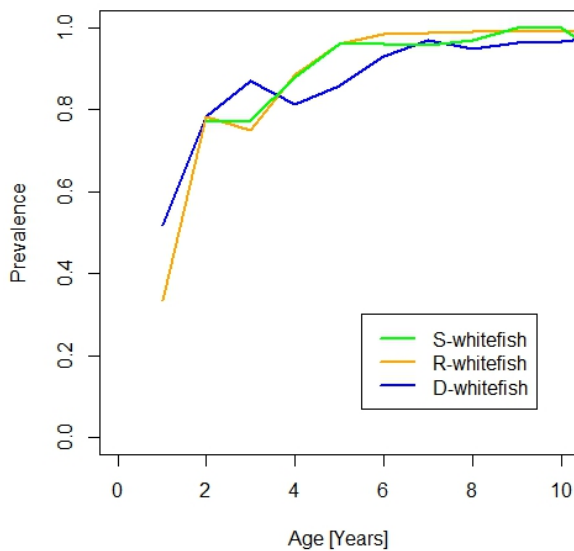

Figure 2. Prevalence of *Diphyllobothrium* spp. in age groups younger than 11 years in three whitefish morphs (S-, R- and D-whitefish) in Lake Femunden.

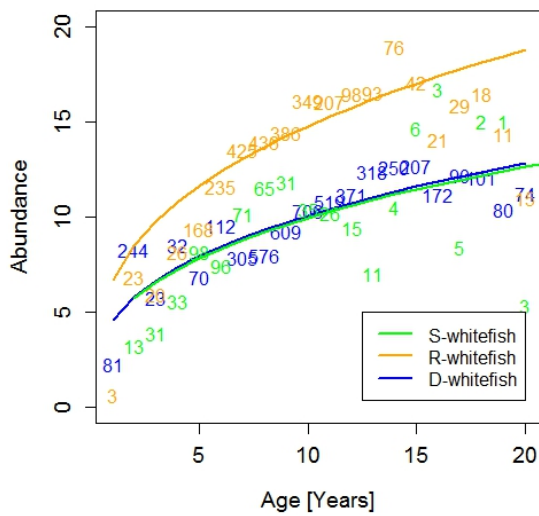**Sandlund, Odd Terje; Næsje, Tor; Diserud, Ola Håvard.**

Figure 3. Illustration of the relationship between age (x) and abundance of *Diphyllobothrium* spp. (y, median no. of cysts per fish, including the uninfected individuals) for three whitefish morphs in commercial and survey net catches from Lake Femunden, 1988-2005. N is number of analyzed fish per age group and morph.

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Table 1. Characteristics of three whitefish morphs in Lake Femunden (from Sandlund et al., 1995; Næsje et al., 1998; 2004; Saksgård et al., 2002).

Characteristics	D-whitefish	R-whitefish	S-whitefish
Asymptotic length (cm)	32.2	38.3	40.5
Age at >50% maturity (male-female)	8-9	7-8	3-5
Gilrakers (modal #)	28	36	43
Gillrakers (range)	23-33	34-40	41-50
Spawning habitat	>30 m in lake	Inlet rivers	<5 m in lake
Adult habitat	Benthic-Pelagic	Littoral benthic-Pelagic	Littoral benthic

Table 2. Generalized linear mixed model (GLMM) for the prevalence of *T.crassus* for the three whitefish morphs D-, R- and S-whitefish in Lake Femunden. Intercept corresponds to D-whitefish with age zero.

Coeffecients	Estimate	SE	z value	Pr(>|z|)
(Intercept)	-2.625	0.137	-19.1	< 2e-16
Age	0.131	0.008	16.2	< 2e-16
R-whitefish	0.731	0.159	4.60	4.2e-16
S-whitefish	1.519	0.225	6.74	1.6e-11
Age : R-whitefish	-0.021	0.015	-1.42	0.156
Age : S-whitefish	-0.060	0.024	-2.53	0.012

Table 3. Generalized linear model (GLM) for the abundance of *Diphyllobothrium* spp. with quasi-poisson error distribution in the three whitefish morphs D-, R- and S-whitefish in Lake Femunden. Intercept corresponds to D-whitefish with age zero.

Coeffecients	Estimate	SE	t value	Pr(>|z|)
(Intercept)	1.517	0.042	35.9	<2e-16
ln(Age)	0.345	0.018	19.7	<2e-16
R-whitefish	0.382	0.016	24.2	<2e-16
S-whitefish	-0.013	0.035	-0.383	0.702