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Parasite-induced host mortality: indirect evidence from a long-term study

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Synopsis

A long-term field study of a perturbed host–helminth system provides indirect evidence that a long-lived swimbladder nematode, *Cystidicola farionis*, induces mortality of Arctic charr, *Salvelinus alpinus*. The prevalence and abundance of this parasite has changed little over the period from 1987 to 1999. The cumulative numbers of L_3-stage larvae steadily increased with increasing host age, indicating a continuous exposure to infection throughout the life of the target fish host. Indirect methods, which used data pooled over years and long-term cohort analyses, indicate that parasite-induced host mortality (PIHM) occurs in hosts older than 10 years. Furthermore, using a short-term cohort method adjusted for worm recruitment, we found indications of PIHM occurrence even in younger age groups. These patterns do not seem to be caused by high parasite mortality rates since dead worms are rarely observed inside the swimbladder. Age-related changes in infection rates or in resistance to infection seem to play only a minor role as there were only slight changes in the preference of charr for feeding on amphipods (which are intermediate hosts) and in the acquisition rate of L_3 larvae in older hosts. Mortality of the most heavily infected hosts is the most probable explanation for the observed patterns.

Introduction

Several studies have shown clear indications that macroparasites can regulate wildlife populations by increasing the mortality rates or reducing the fecundity of their hosts (e.g., Esch 1994, Scott & Tanguay 1994, Gulland 1995, Hudson et al. 1998, Tompkins & Begon 1999). Perhaps the strongest evidence for such parasite–host interactions comes from perturbation studies where both host and parasite populations are not at their equilibrium levels (Quinnell et al. 1990, Tompkins & Begon 1999). Load-dependent parasite-induced host mortality (PIHM) is difficult to demonstrate from field studies (McCallum & Scott 1994, Hudson & Dobson 1995). Indications of PIHM may be obtained indirectly from convex age–intensity curves concomitant with a decline in the degree of parasite dispersion in older host age-classes (Crofton 1971, Anderson & May 1978, Anderson & Gordon 1982, Kennedy 1984). Such indirect evidence of PIHM based on epidemiological patterns has been used several times by combining data from field studies, experimental work, and model simulations (Scott 1987, Esch 1994, Dobson & Hudson 1994, Rousset et al. 1996, Hudson et al. 1998). Nevertheless, other causes may also create peaked age–intensity curves, such as age-related changes in the rate of infections or in the resistance to infections (Anderson & Gordon 1982).

One limitation in using indirect methods for determining PIHM is that fluctuating levels of worm recruitment to the target host population may mask the patterns. This problem may be reduced if the recruitment rates are known. Swimbladder nematodes of the genus *Cystidicola* go through several ontogenetic stages with a distinct recruitment stage (L_3 larvae) and have a life span of several years in their final hosts, fishes of the genus *Salvelinus* (Black & Lankester 1980, 1981, 1984, Giæver et al. 1991). These nematodes are regarded as pathogenic to several salmonid species,

and gross lesions in the swimbladder are apparently caused by chronic mechanical irritations from the presence of large numbers of worms (Lankester & Smith 1980, Black 1984, Snoj et al. 1986, Willers et al. 1991, Moravec 1994). Parasite-induced effects on the fish are dose dependent, as the long life span of *Cystidicola* spp. permits the aggregation of several thousand worms in a single fish (Black & Lankester 1984, Knudsen & Klemetsen 1994).

In Takvatn, North Norway, Arctic charr are heavily infected with *C. farionis*, which have the amphipod *Gammarus lacustris* as the only intermediate host (Giæver et al. 1991, Knudsen & Klemetsen 1994). This lake has been extensively manipulated through a stock reduction program of charr (Klemetsen et al. 1989, 2002, Amundsen et al. 1993), which caused an almost tenfold increase in density of *C. farionis* (Giæver et al. 1991, Knudsen & Klemetsen 1994). An eleven-year data set is available from Takvatn, allowing the possibility of following host cohorts over different intervals (cohort analyses), a powerful tool for the analysis of epidemiological processes of helminthes in host populations. Samples pooled over several years may also reduce the problem of using data sets with inadequate numbers of old surviving hosts (Anderson & Gordon 1982, Hudson & Dobson 1995).

The aims of the present study are: (1) to provide indirect evidence of PIHM using the common traditional methods described by Anderson & Gordon (1982), and (2) to present a new approach, where adjustments are made for fluctuating parasite recruitment to the target host population, thereby reducing the impact new infections have on using indirect methods of determining PIHM. These objectives are achieved by using samples pooled over several years and cohort analyses of macroparasites within an age-structured fish host population that was sampled over several years.

Materials and methods

Takvatn (69°07′N, 19°05′E, 214 m a.s.l.) is a 15-km^2, oligotrophic, 80-m deep lake in North Norway (Klemetsen et al. 1989). The lake contains populations of Arctic charr, threespine stickleback, *Gasterosteus aculeatus*, and a small population of brown trout, *Salmo trutta*. Klemetsen et al. (2002) provide information about the methods used for gill-net sampling of Arctic charr.

A total of 1880 charr were examined for nematodes in the swimbladder (Table 1). The fish were weighed and measured (fork length), and age was determined by the surface reading of otoliths placed in glycerol (Klemetsen et al. 2002). The stomach contents were analyzed and the degree of amphipod feeding was expressed as the frequency of occurrence (%) and prey-specific abundance (for *Grammarus*-feeding charr, the percentage of the total stomach contents made up of *Gammarus*, Amundsen et al. 1996). The swimbladders were preserved in 70% ethanol. Nematodes were classified into four groups according

Table 1. Number of Arctic charr in different age groups examined for *C. farionis* from 1987 to 1999 (n = 1880). Age cohorts used in the long-term cohort analysis are denoted as: α(1977 year-class), β(1978), χ(1980), δ(1981), and ε(1982).

Age	Sampling years									Total
	1987	1988	1991	1992	1993	1994	1995	1996	1997–99	
2	43	17	16	2	1	44	30	19	22	268
3	99	22	60	15	0	36	58	33	23	346
4	184	70	25	21	8	11	20	36	30	405
5	69	63	14	13	10	32	3	26	20	250
6	33	24	8	8	2	47	9	2	10	143
7	16	7	15	9	3	28	15	9	16	118
8	26	8	24	14	3	12	2	5	5	99
9	13	12	18	22	2	12	3	1	2	85
10	9^{α}	7^{β}	12^{δ}	21^{ε}	10	9	1	0	3	72
11	7	7^{α}	6^{χ}	8^{δ}	6^{ε}	14	1	1	0	50
12	2	1	1	9^{χ}	3^{δ}	3^{ε}	1	0	0	20
13	0	0	2^{β}	7	2^{χ}	2^{δ}	0	0	0	13
14	2	1	2^{α}	4^{β}	1	1	0	0	0	11
Total										1880

to Giæver et al. (1991): L_3, L_4 (pre-adult), male, and female adults. The input of parasites to hosts is given by the cumulative number of L_3 larvae (recruitment stage) with increasing age of charr. The cumulative numbers of L_3 larvae are regarded as the lifetime minimum infection level of the long-lived *C. farionis* in the fish host.

Three overcrowded swimbladders from charr (age 9–11 years) with live *C. farionis* (range: 1050–1540 worms) were checked for dead worms: swimbladders were fixed in ethanol and worms were subsequently classified as potentially dead or alive based on morphological differences.

The occurrence of PIHM was explored using the traditional indirect methods described by Anderson & Gordon (1982) and Lester (1984). First, age-related changes in patterns of abundance and variance-to-mean ratios of parasites and frequency distributions of worms were analyzed on data pooled over several years. Next, a long-term cohort analysis was used to survey the parasite density in old hosts from the same age cohort that had been sampled over several years. The selection of cohort year-classes was based on whether: (1) the cohort was sampled on at least three different occasions between the ages of 10 and 14, and (2) there were at least two charr at each sampling (see Table 1). Additionally, we used a short-term cohort analysis that minimizes the effect of fluctuating parasite recruitment from one year to the next. The method follows a cohort of hosts (autumn samples only) over two successive years and assumes that: (1) the life span of worms is several years and the development time from L_3 to L_4 is about two months (Black & Lankester 1980), and (2) both *Gammarus* feeding (the intermediate host) by the charr and the parasite recruitment of L_3 larvae show an annual autumn peak (Giæver et al. 1991, Knudsen & Klemetsen 1994). The change in worm numbers (w) between two successive years for the same cohort of fish is described by:

$$w = (x_{t+1} - L_{3t+1}) - x_t, \quad (1)$$

where x = abundance of parasites in a cohort of hosts in age group (t) or age group (t + 1), L_3 = abundance of *C. farionis* L_3 larvae in a cohort of hosts in age group (t + 1). If there is no change in worm density (w = 0), the total number of nematodes (L_3, L_4, and adults) in a cohort age group (t) will be equal to the number of late-stage nematodes (L_4 and adults) the successive year (t + 1). A positive value (w > 0) means that an additional recruitment of worms has taken place during the late autumn or winter in age group (t). A negative value (w < 0) indicates a loss of worms from the host population from one year to the next.

The parasite infections were compared and tested using χ^2-test, Kruskal–Wallis test, or Mann–Whitney U-test (Systat, version 7.0). Parasitological terms are used according to Bush et al. (1997).

Results

In the sample of charr pooled over several years, feeding on amphipods was highest (34%) for seven-year-old fish and decreased and leveled out to about 20% for the oldest hosts (Table 2). The quantity of amphipods (prey-specific abundance) in the stomachs of the amphipod feeders was stable between 50% and 80% in charr older than five years. The prevalence of *C. farionis* in the pooled fish sample was 93% for four-year-old charr, and only two charr above six years of age were free from nematodes (Table 3). There were no differences in prevalence over the period from 1987 to 1999 in fish of age five or older. An estimate of dead *C. farionis* was made from a limited number of swimbladders (n = 48, range of total number of worms: 2–2102) in charr of 6–13 years old. Potentially dead worms were identified in 37.5% of the swimbladders (range: 112–2048 worms), with a mean proportion of 0.55% (range: 0.2–1.4%) dead worms. No pre-adult or adult worms were observed in charr stomachs or intestines.

Table 2. Amphipod, *Gammarus lacustris*, feeding by Arctic charr: frequency of occurrence in stomach contents (%) and prey abundance (%; for *Gammarus*-feeding charr, prey abundance is defined as the percentage of the total stomach contents made up of *Gammarus*). Data are from a pooled sample (n = 1880) of Arctic charr sampled from 1987 to 1999. See Table 1 for the number of fish in each group.

	Age group										
	2	3	4	5	6	7	8	9	10	11	≥12
Frequency (%)	9	11	19	26	26	34	25	31	19	22	19
Abundance (%)	15	46	47	49	64	59	71	62	57	83	53

Table 3. Prevalence (%) of *Cystidicola farionis* in the pooled sample of Arctic charr. The highest (max) and lowest (min) prevalence in the period 1987–1999 in the respective age groups are given (n = 1880). See Table 1 for the number of fish in each group.

	Age group										
	2	3	4	5	6	7	8	9	10	11	≥12
Prevalence	44	74	93	94	99	100	100	99	100	98	100
Max	77	93	96	100	100	100	100	100	100	100	100
Min	16	31	79	91	96	100	100	95	100	90	100

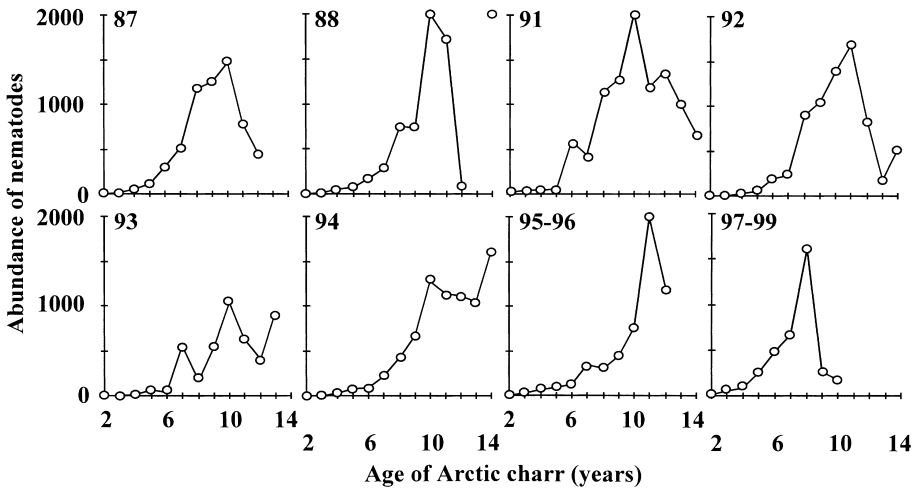

Figure 1. Abundance of *C. farionis* as a function of Arctic charr age in the different sampling years (1987–1999). See Table 1 for the number of fish in each group.

Most age–abundance curves peaked at fish ages of about 10 years (Figure 1). These convex age–abundance patterns also appeared in the pooled samples of nematodes within the charr population (Figure 2). The nematodes were highly aggregated in the host population, with variance-to-mean ratios ranging from several hundred to about two thousand starting in six-year-old fish. The variance-to-mean ratio peaked at age 10 and was generally closely associated with the abundance curve. The input of parasite larvae to hosts (i.e., the cumulative numbers of L_3 larvae) was closely related to the parasite abundance curve up to age 10 in the pooled sample of charr (Figure 2). Thereafter, the cumulative numbers of L_3 larvae continued to increase while the abundance of the pooled sample of *C. farionis* dropped sharply. There was a significant decrease (39.1%) in parasite abundance between charr of age 10 (n = 77) and of age 12 and older (n = 44) (Mann–Whitney U-test, p = 0.045). The frequency distribution of parasites among older hosts (above 10-year-old) indicate a

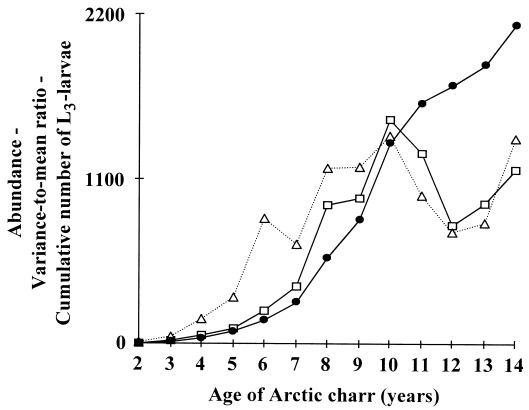

Figure 2. Abundance (squares), variance-to-mean ratio (triangles), and cumulative number of L_3 *C. farionis* larvae (filled circles) as a function of Arctic charr age in the pooled sample from 1987 to 1999. See Table 1 for the number of fish in each group.

reduction of charr with a load of more than 2000 worms (Figure 3). The frequency distribution in 10-year-old

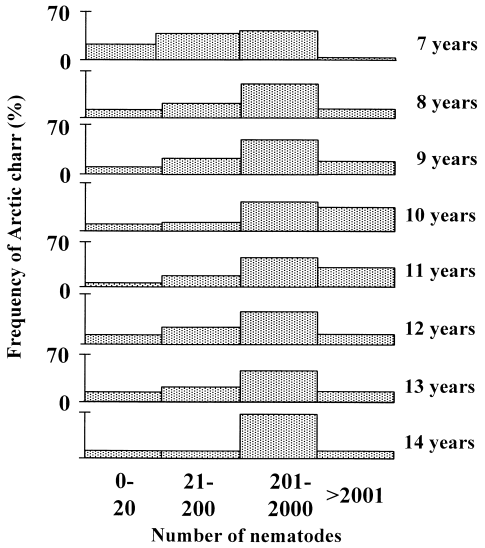

Figure 3. Frequency distributions (%) of *C. farionis* in the pooled sample of Arctic charr of different age groups in the period from 1987 to 1999. See Table 1 for the number of fish in each group.

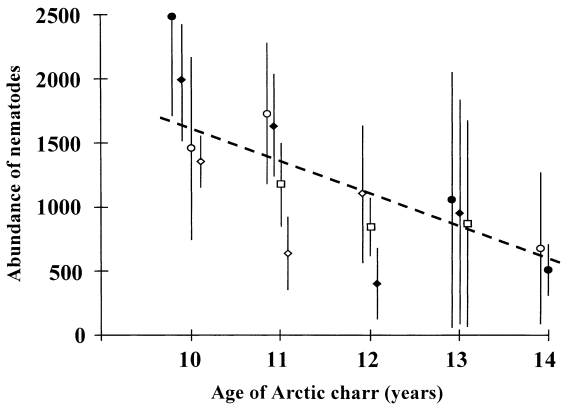

Figure 4. Abundance (±SE) of *C. farionis* with increasing fish age in five cohort year-classes of Arctic charr: 1977 (open circles), 1978 (filled circles), 1980 (squares), 1981 (filled diamonds), 1982 (open diamonds). See Table 1 for the number of fish in each group. Regression equation: $y = -299.6x + 4702.6$, $r^2 = 0.51$, $p < 0.001$.

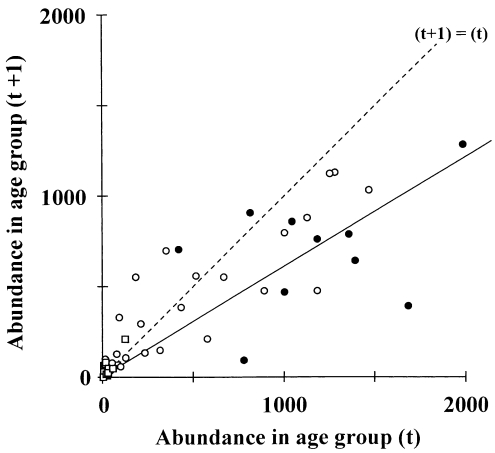

Figure 5. Plot of abundance of *C. farionis* between two successive age groups (t and t + 1) in different cohort year-classes of Arctic charr. Age group (t) is given by: 2–5 years (squares), 6–9 years (open circles), 10 years and older (filled circles). See Table 1 for possible cohort age group combinations (n = 59). Regression equation: $t + 1 = 0.63t$, $r^2 = 0.70$, $p < 0.001$.

fish (n = 72) was not significantly different than that of hosts of 12 years and older (n = 44) (χ^2-test, $p > 0.05$).

In the analyses of five cohorts (1977, 1978, 1980, 1981, 1982 year-classes, Figure 4), there was a significant decrease in parasites in charr older than 10 years of age (Kruskal–Wallis, p = 0.041, n = 103). In the short-term cohort analysis adjusted for parasite recruitment (L_3 larvae), observations below the dotted line indicate that parasites are lost from the charr population between two successive years (Figures 5, 6). A reduction in the number of heavily infected hosts was apparent with increasing worm intensities in age group (t), but reductions in infection occur even in middle-aged groups and at lower infection intensities of about 500 worms (Figure 5). The linear regression ($y = 0.63x$, $r^2 = 0.70$, n = 59) between abundance in year (t + 1) and year (t) was significantly different from a slope of 1 (slope: 0.63 ± 0.08; 95% CI). By arranging these data with increasing age of charr, a reduction in parasite intensities between two successive years, (t + 1) − (t), is observed from age six (Figure 6).

Discussion

The two methods used, pooling samples over several years and long-term cohort analyses offer indirect evidence that PIHM may be the cause of the observed pattern of declining worm intensities in older hosts. This is not surprising, as the abundance of swimbladder nematodes in the charr population was very high and stable throughout the entire study period. Typically, when *Cystidicola* spp. are present, they tend to be locally stable with high intensities in charr populations (Black 1985, Giæver et al. 1991,

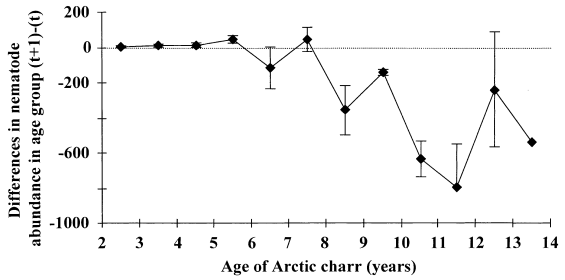

Figure 6. Differences in abundance (±SE) of *C. farionis* between two successive age groups ((t + 1)–(t)) in the same cohort year class of fish as a function of increasing age of Arctic charr. See Figure 5 and Table 1 for possible cohort age group combinations (n = 59).

Knudsen & Klemetsen 1994, Knudsen 1995). Amphipods are generally attractive prey items for charr, which ensures efficient transmission of parasite larvae, although the infection levels in the intermediate host were low during the entire study period (Amundsen 1989, Knudsen & Klemetsen 1994, Knudsen et al. 1996, 1999). The observed long-term stability of host–parasite relationship in our study indicates that a density-dependent feedback mechanism such as PIHM may be involved (Anderson & May 1978). Black & Lankester (1984) suggested that retarded growth and reduced fecundity of worms in heavily infected charr are important factors involved in minimizing fluctuations in *Cystidicola* spp. populations. The convex age–abundance curve implies that the most heavily infected fish disappear from the population, as has been found in several other studies (e.g., Pennyquick 1971, Gordon & Rau 1982, Kennedy 1984, Esch 1994). These epidemiological patterns are supported by the analyses of sequential samples of host cohorts, which show in detail that the old surviving hosts have lower nematode intensities.

Convex age–abundance curves could be generated by biological processes other than PIHM, such as age-dependent changes in infection rate and development of resistance to infection through either reduced macroparasite survival and-or establishment of parasite larvae (Anderson & Gordon 1982). However, age-dependent changes in exposure to parasites seem less likely in our study since the proportion of amphipod feeders and quantities of amphipods ingested were relatively constant in the older host age-classes. Therefore, larger old hosts also consume amphipods in high numbers, as reflected by the relatively large number of L_3 larvae present in old fish. Alternatively, the high numbers of L_3 larvae in old charr that we observed in our study could be caused in part by arrested development of larvae, as has been observed in nematode larvae that are parasites in eel swimbladders (Ashworth & Kennedy 1999). However, density-dependent retardation of development seems low because the cumulative numbers of L_3 larvae were always below the age–abundance curve of *C. farionis* up to age 10 and should be even less significant with the reduced nematode densities observed in the large-sized older hosts.

The observed dense infra-populations of worms in charr should theoretically reach sizes at which parasite survivorship would become negatively affected (e.g. Brown 1986). In experimental studies, no dead *Cystidicola* spp. were found after two years in the swimbladder, and this parasite is thought to live at least 10 years in charr (Black & Lankester 1980, 1984, Black 1985, Giæver et al. 1991, Moravec 1994). We found only a small fraction of dead nematodes even in overcrowded swimbladders, which is similar to observations reported in other field studies (Black & Lankester 1981). Arctic charr is a physostome fish, but there was apparently no movement out of the swimbladder when charr worm burdens were high, as no pre-adult or adult worms (live or dead) were ever found in the charr gastrointestinal tract. Thus, the long life span permits the aggregation of large worm numbers, which may lead to chronic infections and morbid fish.

Experimental studies have shown that the development of acquired immunity can be a major factor in causing convex abundance curves in mammalian hosts (Quinnell & Keymer 1990, Grenfell et al. 1995). Teleost fish immunology resembles that of mammals in many respects, but the protective function against helminths other than monogeneans is still inconclusive for fish (Secombes 1994). Specific immune responses against swimbladder nematodes of eel are partly known from experimental studies (Knopf et al. 2000b), but the importance of immunity on epidemiological patterns in field studies is uncertain because of the high variability in other host traits (Wakelin 1984, Quinnell et al. 1990). The observed high density of L_3 larvae in old fish suggests low resistance to re-infections, and immune unresponsiveness against invading larva swimbladder nematodes has been observed in eel (Knopf et al. 2000a). Thus, there seem to be low density-dependent constraints on the establishment of L_3 larvae. In contrast, adult swimbladder nematodes in eels seem to be able to elicit specific antibodies (Knopf et al. 2000a,b). However, the low proportion of dead adult worms observed in our study suggests

that parasite mortality contributes only slightly to the observed peaked age–abundance patterns.

Moravec (1994) regards *Cystidicola* spp. as a highly pathogenic species, but high densities of *Cystidicola* spp. in other charr studies show only weak indications of PIHM (Black 1985, Giæver et al. 1991, Knudsen & Klemetsen 1994). This may be attributed to methodology problems such as a lack of sufficient data from old hosts and high recruitment of worms that may veil the epidemiological patterns. In our long-term study, both the pooled data, with an adequate number of old fish, and the long-term cohort analyses that suffer partly from a few hosts, suggest that the most heavily infected fish disappear. Furthermore, the short-term cohort approach adjusted for parasite recruitment suggests that heavily infected middle-aged charr may also suffer from PIHM. Apparently, this short-term cohort approach may also be a useful method for detecting PIHM in the more numerous young host age groups. This method will overestimate reductions in worm densities between two successive years if retarded development of L_3 larvae occurs frequently, and these possible relations should be tested experimentally.

The Takvatn charr are infected with 11 macroparasite species in total (Kristoffersen 1995). Swimbladder nematodes share a transmission pathway via amphipods with the highly pathogenic adult cestode *Cyathocephalus truncatus* and are also heavily infected by pathogenic *Diphyllobothrium* species (Vik 1958, Henricson 1978, Curtis 1984, Knudsen & Klemetsen 1994). Consequently, the intensities of different worm species may be highly correlated in individual charr (Knudsen 1997) and most likely have synergetic effects that influence the observed epidemiological patterns. In Takvatn, the number of old specimens in the charr population decreased from the mid-1980s until 1995 (Klemetsen et al. 2002), and evidently the few surviving old fish had low nematode densities. The abrupt increase in worm intensities between 1985 and 1987 (Knudsen & Klemetsen 1994) may thus have increased the mortality rates of hosts and enhanced the decline in the number of old charr. Parasites may increase mortality rates of their hosts either directly or indirectly, e.g., by increasing their susceptibility to predation. But predation from piscivorous fish or birds is probably low because even middle-aged fish are large (Klemetsen et al. 2002). In addition, gill nets are prohibited and there is very little angling activity in Takvatn. It has been suggested that Arctic charr suffer from PIHM related to spawning or overwinter mortality (Giæver et al. 1991, Kolasa & Curtis 1996).

The intensities of *C. farionis* infra-populations seem to be strongly associated with the foraging behavior (i.e., individual feeding specialization) of charr on amphipods in Takvatn and elsewhere (Knudsen 1995, Knudsen et al. 1996). The variability in feeding habits may lead to a wide dispersion of parasites in host populations (Crofton 1971, Anderson 1976). The high aggregation of nematodes in our study suggests that the risk of PIHM and morbidity is spread unevenly within the charr population. The most specialized amphipod-feeding charr are repeatedly re-infected and harbor dense infra-populations of worms (Knudsen 1997) and perhaps suffer a high risk of PIHM. Even though specialized foragers may feed more effectively that generalized feeders (e.g., Robinson et al. 1996, Hatfield & Schluter 1999), the higher energetic gain may be outweighed by the higher cost resulting from parasite infections.

The regulatory effects that parasites have on host populations are controversial (Scott & Dobson 1989). However, long-term field studies combined with experimental studies indicate that helminths may regulate host populations (Quinnell et al. 1990, Esch 1994, Dobson & Hudson 1994, Scott & Tanguay 1994, Hudson et al. 1998, Tompkins & Begon 1999). Takvatn has been extensively manipulated through a stock reduction program of Arctic charr, and both parasites and fish populations have been perturbed from their former equilibrium (Klemetsen et al. 1989, 2002, Giæver et al. 1991, Amundsen et al. 1993, Knudsen & Klemetsen 1994). The intensities of *C. farionis* have, according to our study, stabilized at levels nearly 10 times higher than those found in earlier studies (Giæver et al. 1991). The strongest evidence for regulation of host populations by parasites comes from perturbation studies (Tompkins & Begon 1999). Our study does not, however, attempt to estimate the proportion of hosts that might have been removed by high nematode intensities, and the regulatory effect on the charr population is uncertain.

In conclusion, the present study presents indirect evidence that the nematode *C. farionis* may increase mortality rates of its final host, Arctic charr. However, the degree of regulation that this nematode has on the fish population remains uncertain.

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