

Ichthyocotylurus erraticus (Digenea: Strigeidae): factors affecting infection intensity and the effects of infection on pollan (*Coregonus autumnalis*), a glacial relict fish

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SUMMARY

Lough Neagh pollan are heavily infected with the strigeid *Ichthyocotylurus erraticus*, with 100% prevalence and median infection intensities of 600+ metacercariae in the pericardial cavity of mature fish. Female fish were more heavily infected than males. Infection intensity, which rose in summer, varied with pollan size, year, sampling bay within the lough and water depth within bays. Heavily infected pollan were caught further offshore than lightly infected fish. Spatial variation in pollan infection intensity corresponded to variation in the abundance of the first intermediate host, *Valvata* snails. The data suggest that heavily infected fish had lower food intakes. Parasitism reduced condition and liver size in male fish but condition in heavily parasitized females increased. Infection intensity was greater in larger fish of a given age. These patterns are discussed in the context of risks and rewards. The data suggest that inshore waters in summer are the preferred habitat of pollan and that the greater infection intensity of offshore fish results from their reduced competitive ability as a consequence of parasitism and the increased risk of infection there.

Key words: risks, rewards, spatial and temporal variation.

INTRODUCTION

Aggregated distributions of parasites across hosts have been attributed to aggregated distributions of parasites in time (across seasons or years) and space (patchy host distributions) and to variation in host susceptibility due to behavioural, physiological and/or immunological differences (Hudson *et al.* 2002). Frequently, the spatial distributions of parasitized and unparasitized hosts differ. The hypotheses proposed to account for these spatial differences can be fitted into a framework of trade-offs between risks and rewards to hosts and/or parasites. If hosts are unable to recognize the risk of being parasitized or if this risk is uniform across habitats then infection intensity should correlate with the distribution of the infective agent. Alternatively, if they can detect such risks, and these vary spatially, hosts should occupy the low risk habitat. If parasites affect host fitness by reducing competitive ability then parasitized hosts would be most likely to occupy the low reward habitat. Parasite manipulation of host habitat selection, either evolved or incidental, to increase transmission to the next stage of the life-cycle has been widely discussed (Holmes and Bethel, 1972;

Lafferty, 1999; Poulin, 2000). Such manipulation would be most likely to occur if there is appreciable variation in transmission risks to fish across habitats. For example, parasitized fish are more frequently found in inshore waters (Holmes and Bethel, 1972; Bean and Winfield, 1992; Loot *et al.* 2001), increasing their susceptibility to piscivorous birds, which are often the final hosts of the parasites. Note that the increased risk to the host constitutes the reward to the parasite. Here we examine spatial and temporal variation in infection intensity of pollan (*Coregonus autumnalis*) by the trematode *Ichthyocotylurus erraticus* within a risk and reward framework.

Pollan is a fish species of high conservation value in Europe since only 4 populations occur, all in Irish lakes (Harrod *et al.* 2002). Three of these populations are small and probably in the terminal stages of decline. Only the Lough Neagh population is large but it too is subject to a variety of threats. As part of a long-term study of pollan ecology, we are examining the potential role of these threats in regulating this population. Pollan in L. Neagh are attacked by several parasites, the most numerous of which is *I. erraticus*. This parasite has been noted in the lough by earlier workers but there has been no previous assessment of its intensity or impact on pollan. However, Harrod and Griffiths (2005) have shown that *I. erraticus* affects gonad size and symmetry in pollan.

L. Neagh is a large (surface area 383 km²), shallow (mean depth 8.9 m), and hypertrophic water body

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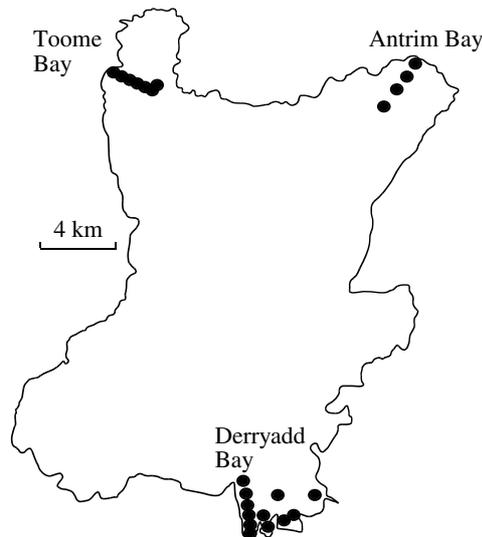


Fig. 1. Outline map of Lough Neagh showing the bays and approximate locations of the sites sampled for fish and *Valvata* spp. The area named here as Derryadd Bay consists of that bay and three others.

and there are within-lake differences in environmental conditions as a consequence of differences in wind exposure, water depth and human activities (Wood and Smith, 1993). This within-lake variability in physical and chemical conditions is reflected in variation in the distribution of *I. erraticus*' first and second intermediate hosts, *Valvata* snails and pollan. This paper examines some of the factors potentially affecting parasite intensity in pollan and the effects of infection on pollan distribution, size, growth and condition.

MATERIALS AND METHODS

Pollan were sampled from 3 bays in Lough Neagh ($6^{\circ}25'W54^{\circ}35'N$) (Fig. 1) during 1998 and 1999 using multipanel survey gillnets (modified S-type, Lundgrens Fiskredskapsfabrik). Pollan were sampled at approximately monthly intervals in Toome Bay from sites with water depths of 1.5, 3, 6, 9, 12, 15 and 20 m: at water depths of 9 m or more the 1.8 m deep nets were set both at the surface and bottom. Fish were collected at 3, 6, 9 and 12 m in Antrim Bay at approximately 3-month intervals. In both of these bays water depth was an indicator of distance from the inshore habitat. Fish were also sampled at approximately 3-month intervals in Derryadd Bay but the depth range was more restricted (most sites were less than 5 m in depth). Pollan catches are expressed as number net⁻¹. As parts of other projects (Bigsby, 2000; Carter and Griffiths, 2001) the benthic fauna was sampled at all sites with a Kajak corer, internal tube diameter 5 cm: numbers of *Valvata piscinalis* and *V. macrostoma*, the first intermediate hosts of *I. erraticus*, were counted core⁻¹. Five cores per site were taken on each occasion.

Fish mass was used as a measure of body size. The contents of the pollan body cavity were separated into gonads, liver, alimentary canal and stomach and each weighed to the nearest 0.01 g. We used gutted mass i.e. (total body mass – body cavity content mass) when examining relationships between body cavity components. Gut contents were not removed from the alimentary canal or stomach before weighing. Gut content mass was estimated by regressing stomach + content mass against the mass of gutted fish on the assumption that stomach mass was a function of fish size and was not affected by infection intensity. While this assumption is questionable, the conclusion is consistent with other direct measures of gut content mass (see Discussion section). Sex was assessed through visual inspection of the gonads. Pollan hearts and any encysted *Ichthyocotylurus* metacercariae found in the pericardial cavity were stored in 80% alcohol. To measure infection intensity cysts were teased from the heart and host reactive tissue using mounted needles and this material squeezed between microscope slides before counting cysts under a low-power microscope.

0+ pollan first appear in the lough around March 15 each year and this date was taken as the birth date. Fish were aged to years from scales and age in days determined as the difference between their date of birth and day of capture. They were allocated to 200-day age-class intervals when calculating prevalence and intensity frequency distributions: a given age class consisted of more than 1 year class i.e. this is a vertical study. Within each age class fish with infection intensities greater than the 80th percentile or less than the 20th percentile were classified as heavily and lightly infected respectively. In some analyses, and because the infection intensity frequency distributions were not normally distributed, medians were calculated as a more robust measure of location. If used in regressions, medians were weighted by the square root of sample size. When necessary data were normalized or linearized by log₁₀ transformation. Since body components and infection intensity varied with body size the effects of the latter were controlled for by partial correlation. Fish somatic condition was assessed as deviations from log body mass – log length regressions i.e. the allometric condition factor (Ricker, 1975) was used. To test for an effect of infection intensity on condition regression lines for heavily and lightly infected fish were tested for differences in slopes and intercepts.

RESULTS

Most encysted metacercariae of *I. erraticus* were found around the heart but only rarely elsewhere. Aggregated cysts were typically enclosed by host reactive tissue and in the most heavily infected hosts this appeared to constrain the elasticity of the

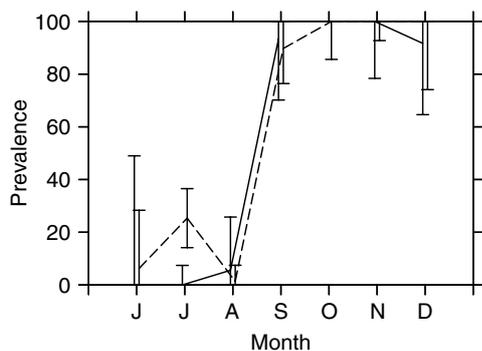


Fig. 2. Seasonal variation in the mean percentage ($\pm 95\%$ CI) of 0+ pollan infected by *Ichthyocotylurus erraticus* in 1998 (solid line) and 1999 (dashed line). Median number of fish examined was 18 month^{-1} (range 4–72).

heart. The infection was sometimes so extreme that the ventricle of the heart was hidden under several layers of cysts and connected to the pericardial membrane by cysts. In most fish the metacercariae were either embedded in ventricular tissue or found in large aggregations on the ventricle and bulbus arteriosus.

There was a marked seasonality in the prevalence of infection in 0+ fish (Fig. 2), rising from a mean of 9% ($n=229$) in June–August to more than 96% ($n=164$) in September–December. Of the 1+ and older pollan in Lough Neagh ($n=2126$) 99.9% were infected with metacercariae of *I. erraticus*.

The variance/mean ratio was always significantly greater than 1, i.e. the parasites were aggregated across hosts, but this ratio did not change with age e.g. the slope of the log variance–log mean relationship was not significantly different from 1.0 ($b=0.95 \pm 0.07$, $n=8$). Apart from fish in the youngest age class the infection intensity distributions were not significantly different from the negative binomial distribution (mean $k=2.4$ for 2+ and older fish).

Infection intensity (log transformed) increased with age at the same rate in both sexes (2+ fish and older, $F_{1,773}=0.90$, $P=0.34$) but was greater in females than in males ($F_{1,774}=17.75$, $P<0.001$; geometric means 526, 408 respectively). This difference remained after body size (log W) was included in the analysis.

Temporal and spatial variation in infection intensity in pollan

Infection intensity was relatively low until the second year of life (Fig. 3) when it rose rapidly over the summer period. This summer increase more or less corresponded to the period when water temperature exceeded 13°C (June–October) (Fig. 4) and for fish of the 1997 year class the median infection intensity in late 1999 (490 fish^{-1}) was 15-fold greater than that in the 1998/9 winter period (33 fish^{-1}).

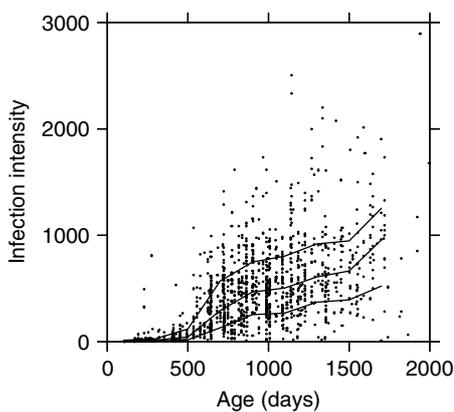


Fig. 3. Infection intensity as a function of fish age (see Materials and Methods section for details of the age calculation). The median, 20 and 80 percentiles are superimposed on the plot (using a 200 day age class interval).

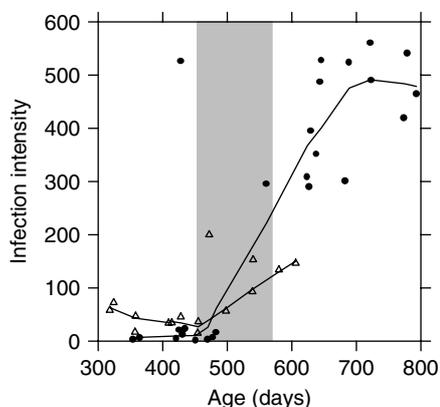


Fig. 4. Change in the median infection intensities with age of fish of the 1997 (circles) and 1998 (triangles) year classes. The approximate period when water temperature was greater than 13°C in 1998 and 1999 is shaded. The lines are fitted by locally weighted scatterplot smoothing.

Subsequently there was little indication of seasonal variation in parasite intensity, which increased at a rate of about $133 \pm 28 \text{ year}^{-1}$. Median infection intensity in mature fish was around 600 but one 3+ female caught in May 1999 had 3941 cysts. Infection intensity increased more rapidly over the summer in the 1997 year class than in the 1998 year class (Fig. 4; slopes, $F_{1,11}=10.74$, $P<0.01$).

Infection intensity varied spatially and across years: the analysis excluded 0+ fish because infection intensity varied strongly seasonally. An ANOVA of log infection intensity with bay and year as factors and body size (log mass) and water depth as covariates (Table 1) showed significant differences between years, between bays, a significant effect of depth (Fig. 5) and a significant interaction between year and bay. Infection intensity in both Toome and Antrim Bays was significantly higher in 1999 than 1998 but showed a small, non-significant, decline in Derryadd Bay.

Table 1. ANOVA of *Ichthyocotyurus erraticus* infection intensity (\log_{10} transformed) in 1+ and older pollan as a function of year of sampling, bay, depth within bay and body size (W)

($R^2=0.52$. Adjusted least squares mean intensities are shown for each year and for each bay.)

Variable	D.F.	MS	F	P
Year	1	2.285	17.37	<0.001
Bay	2	0.947	7.20	0.001
\log_{10} W	1	100.652	764.81	<0.001
Depth	1	6.215	47.23	<0.001
Bay*Year	2	1.885	14.33	<0.001
Error	879	0.132		

Adjusted least squares means

	Infection intensity \pm S.E.	n
1998	167 \pm 26.1	255
1999	327 \pm 24.3	632
Toome	313 \pm 12.2	660
Antrim	187 \pm 44.6	86
Derryadd	218 \pm 24.4	141

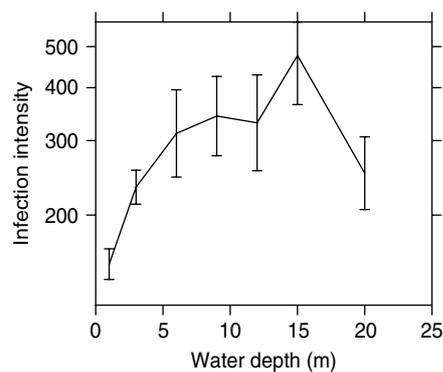


Fig. 5. Mean infection intensity (\pm 95% CI) (on a \log_{10} scale) in Toome Bay in 1999 as a function of water depth at the sampling sites. Depth is a surrogate for distance from shore.

Heavily infected fish of a given age class were consistently found further offshore (at deeper sites) than lightly infected individuals ($F_{1,435}=33.42$, $P<0.001$) (Fig. 6). The correlation between infection intensity and distance offshore still remained after the effect of body size ($\log W$) was controlled (partial $r=0.23$, D.F. = 574, $P<0.001$).

Spatial and temporal variation in the distribution of pollan

In Toome Bay the biomass of pollan caught in the summer (water temperature $>13^\circ\text{C}$) was independent of sample site depth for surface-caught fish ($F_{1,42}=0.03$) and 3.3 times greater than that of fish caught in bottom-set nets ($F_{1,48}=16.60$, $P<0.001$). Surface-caught pollan were more numerous but

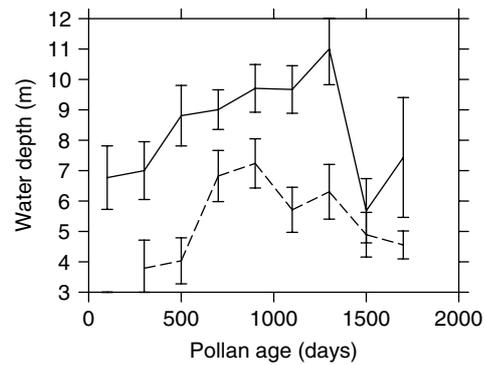


Fig. 6. Mean depth (\pm S.E.) at which heavily (solid line) and lightly infected (dashed line) pollan of different ages (200 day age class intervals) were caught in Toome Bay. Depth is a surrogate for distance from shore.

smaller than bottom-caught fish (mean number net^{-1} 13.5 v 3.5 $F_{1,48}=25.26$, $P<0.001$; mean mass 92 v 110 g $F_{1,48}=4.29$, $P=0.04$).

There were significant differences in pollan biomass across bays and years ($F_{2,53}=4.71$, $P=0.01$ $F_{1,53}=4.63$, $P=0.04$ respectively), in pollan numbers across bays ($F_{2,53}=4.53$, $P=0.02$) and in mean size across years ($F_{1,53}=3.95$, $P=0.05$). Pollan numbers and biomass were greatest in Antrim Bay and least in Derryadd Bay and greater in 1998 than in 1999.

Stomach mass (including contents) increased with the gutted mass of surface caught pollan but decreased with increasing distance offshore (depth of the sample site) (Table 2). Inclusion of infection intensity as a predictor variable led to a marginal improvement in variance explained but partial correlation, after controlling for body size and depth, showed no effect of infection ($r=0.03$, 482 D.F.).

Spatial and temporal variation in the abundance of Valvata

Valvata abundance differed between bays, between months and with water depth but there was no difference between years and no significant interaction between water depth and bay (Table 3). There were significant increases in *Valvata* abundance from Antrim Bay to Derryadd Bay to Toome Bay (Tukey HSD test, geometric means core^{-1} 0.0 \pm 0.06, 0.50 \pm 0.05, 1.27 \pm 0.15 respectively). *Valvata* were most abundant towards the end of the calendar year, with numbers dropping to a low in August (Fig. 7).

Infection intensity and pollan performance

I. erraticus infection affects the mass-length relationship in both male and female pollan, but in different ways. In males parasitism reduced condition by a constant proportion (the regression slopes were parallel) (Table 4). This result occurred whether total mass, somatic mass or gutted mass was the dependent variable and the parasite effect, while

Table 2. Multiple regression slopes of \log_{10} stomach mass (and contents) as a function of gutted fish mass and water depth of site ($R^2=0.78$, $n=491$)

Variable	Slope \pm S.E.	<i>t</i>	<i>P</i>
$\log_{10} W_{\text{gutted}}$	0.79 ± 0.019	41.02	<0.001
Depth	-0.005 ± 0.001	4.44	<0.001

Table 3. ANOVA of *Valvata* numbers core^{-1} ($\log_{10} x + 1$ transformed data) as a function of year of sampling, bay and depth within bay

(The first three variables were treated as factors. $R^2=0.21$.)

Variable	D.F.	MS	<i>F</i>	<i>P</i>
Year	1	0.010	0.13	0.72
Month	9	0.796	9.70	<0.001
Bay	2	4.861	59.23	<0.001
Depth	1	0.444	5.41	0.02
Error	1090	0.082		

weak, remained after the dominant effect of length was controlled for by partial correlation (e.g. gutted mass partial $r = -0.12$, 293 D.F., $P < 0.05$). Parasitism affected the slope of the length-mass relationship in females and large, heavily parasitized fish were heavier than lightly parasitized fish of the same length (Fig. 8). The same conclusions were reached when infection intensity was included as a variable (Table 4).

After body mass was controlled for, liver size was negatively correlated with infection intensity in male but not in female fish (e.g. gutted mass, partial $r = -0.17$, 343 D.F., $P < 0.05$, partial $r = -0.03$, 372 D.F., respectively).

Piecewise regression of the complete dataset showed that pollan growth rates (mass – age regression slopes) changed slope at $582 \pm 95\%$ CI 30 days (Fig. 9). Despite an approximately 8 to 10-fold difference in parasite intensity the growth rates of the most and least heavily infected fish were similar (Fig. 9). The growth rate declined once pollan mass reached about 100 g (104.3 g, 101.4 g in heavily and lightly infected fish respectively) but heavily infected fish reached this size in $561 \pm 95\%$ CI 28 days compared to 665 ± 35 days for lightly infected individuals. Multiple regressions showed that fish mass was significantly predicted by infection level, age (years) and water depth for both growth rate groups of fish. Partial regressions showed significant positive correlations between fish size and infection level after controlling for the effects of age and water depth i.e. bigger fish of a given age had higher infection intensities (age < 561 days $r = 0.21$, 82 D.F., $P = 0.06$, age > 665 days $r = 0.15$, 317 D.F., $P < 0.01$).

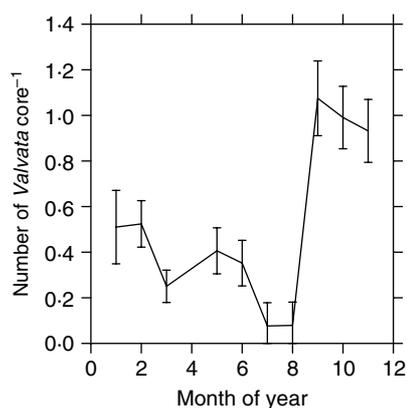


Fig. 7. Seasonal trend in the least squares adjusted mean number (\pm S.E.) of *Valvata* core^{-1} across all years, sites and bays. The corresponding ANOVA is shown in Table 3.

DISCUSSION

While *I. erraticus* can complete its life-cycle in the laboratory in 10–12 weeks at 20 °C (Olson, 1970), Swennen, Heessen and Höcker (1979) suggested that it takes 1 year in nature. *Valvata* species are the only recorded first intermediate hosts. These release cercariae over several months in the summer (Olson, 1970; Swennen *et al.* 1979). The cercariae are released in daylight (Bell, Sommerville and Gibson, 1999) and increase swimming activity in response to shadows (Swennen *et al.* 1979), suggesting that infection of the second intermediate host is more likely to occur in the surface waters of L. Neagh since little light penetrates below 2 m in summer. *I. erraticus* has been recorded from a variety of salmonid fishes: in L. Neagh it has only been identified from pollan though Faulkner, Halton and Montgomery (1989) found *I. variegatus* in perch. A wide range of aquatic birds have been examined as possible definitive hosts but infections found only in gulls of the genus *Larus* (Niewiadomska and Kozika, 1970; Swennen *et al.* 1979) and not in cormorants or great-crested grebes, the two common piscivores in L. Neagh. The usual method of transmission to the definitive host is unclear. Cramp and Simmons (1983) noted that black-headed gulls (*Larus ridibundus*) will take 'fish of shallow water or swimming just below the surface, also sick and dead individuals'. Black-headed gulls were observed scavenging on pollan discarded by commercial fishermen: the gulls consumed eyes, gills and heart first (C. Harrod, unpublished observations). *I. erraticus* typically show close to 100% prevalence and high infection intensities in fish (Olson, 1970; Dolezel and Crompton, 2000; Karvonen and Valtonen, 2004): infection intensities in pollan in L. Neagh are typical in this regard although rather higher than those recorded for *C. lavaretus* in Finland and L. Lomond. High infection intensities have occurred in L. Neagh pollan over a number of years (Gaffikin, 1939;

Table 4. Regressions of the mass-length (W - L) slopes for the most and least heavily infected fish: P slopes is the probability that the W - L slopes for heavily and lightly infected fish are the same. The multiple regressions show the significant terms for pollan mass as a function of fish length and infection intensity (all variables \log_{10} transformed)

(The analysis was restricted to fish collected from Toome Bay.)

	Infection level	W - L statistics			Multiple regression statistics					
		slope \pm s.e.	n	P slopes	Variable	slope \pm s.e.	t	P	R^2	n
Males	Heavy	3.26 ± 0.24	54	0.48	L Infection intensity	3.25 ± 0.09	37.97	< 0.001	0.84	297
	Light	3.07 ± 0.14	56			-0.01 ± 0.007	2.17	0.03		
	All									
Females	Heavy	3.79 ± 0.26	73	0.02	L Infection intensity $L \times$ Infection intensity	1.87 ± 0.73	2.58	0.01	0.78	303
	Light	2.96 ± 0.23	44			-1.28 ± 0.61	2.08	0.04		
	All					0.54 ± 0.26	2.09	0.04		

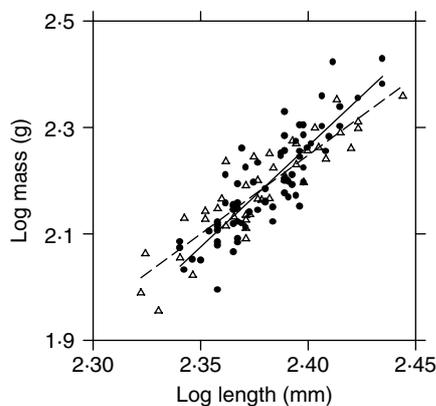


Fig. 8. \log_{10} mass- \log_{10} length regressions for heavily (filled circles, solid line) and lightly (triangles, dashed line) infected female pollan. The corresponding ANOVA is shown in Table 4.

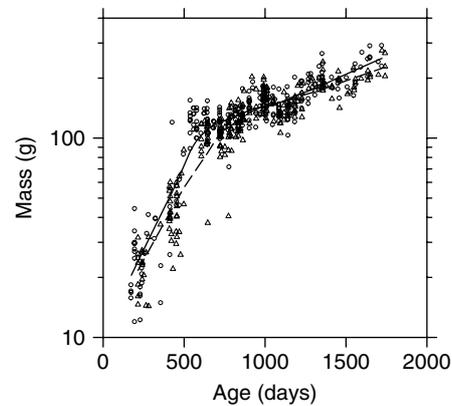


Fig. 9. Body mass (on a \log_{10} scale) at age for pollan heavily (circles, solid line) and lightly (triangles, dashed line) infected with *Ichthyocotylurus erraticus*. The lines are fitted by locally weighted scatterplot smoothing.

Vickers, 1951; T. Pitcher, personal communication). Hence all birds feeding on pollan are likely to be exposed to the parasite.

Infection risk

Swennen *et al.* (1979) noted that water temperatures needed to be at least 13°C before *I. erraticus* cercariae were released from *Valvata* and this is consistent with field observations (Olson, 1970; Wootten, 1973). Water temperature in L. Neagh reached 13°C in mid-June and remained above that temperature until early and mid-October of 1998 and 1999 respectively (D. Griffiths, unpublished observations). However, 1998 was a distinctly cooler year than 1999 (188 *vs* 334 day degrees above 13°C ; D. Griffiths, unpublished observations) and, in line with expectation, infection intensity in pollan was significantly lower in 1998.

Seasonal variation in infection intensity in pollan would be expected to vary with the supply of cercariae by the first intermediate host (*Valvata* species: Olson, 1970; Swennen *et al.* 1979; Bell *et al.* 1999). Infection levels in pollan will depend on the number of cercariae released per *Valvata* and the number of snails. *Valvata* distribution varied across bays and with depth within bays. Data collected by Bigsby (2000) showed peak densities of *Valvata* in Toome Bay in deep water (15+ m) on soft sediments. Peak densities also occurred in the deeper water in the Derryadd Bay area, though this was still shallow (4–5 m) and had a hard substratum. Infection intensities of pollan showed a similar spatial distribution, consistent with infection levels being determined by the supply of cercariae. This pattern, evident even in fish that had received most of their parasites (2 or more years old), suggests that pollan do not show marked movements between sites.

Cercariae have been reported to be active for about 16 h at 22 and 26 °C (Olson, 1970; Swennen *et al.* 1979), and 'slightly longer' at lower temperatures. The limited period that this stage is active, coupled with the localized distribution of the first intermediate host suggests that there may well be spatial variance in infection risk for pollan.

The rapid rise in infection intensity in fish in their second year of life probably reflects an extrinsic effect rather than some intrinsic increase in fish vulnerability since there were marked differences in infection intensity between fish of this age in the 1997 and 1998 year classes. The rise in infection intensity with age corresponded to a shift of older pollan to offshore habitats, locations where the first intermediate host is more common. However, even within an age class the most heavily infected fish were found further offshore than lightly infected fish.

Host risks and rewards in L. Neagh

Bean and Winfield (1989, 1992) found that most roach and gudgeon in L. Neagh occurred inshore in the summer. Kirkwood (1996) showed that most roach, pollan and perch occupied inshore waters in summer, that zooplankton densities were greatest in these inshore waters and that fish gut fullness was greater there. Our data support this finding for pollan. If, as seems likely, small fish outcompete large when feeding on zooplankton (see, for example, Cryer, Peirson and Townsend, 1986; Hamrin and Persson, 1986) inferior competitors are more likely to be found offshore, in locations where they are more likely to become parasitized (though cause and effect are hard to separate). Note that all ages of pollan feed predominantly on zooplankton in summer i.e. the offshore move of larger fish is not associated with an ontogenetic dietary shift.

Bean and Winfield (1989, 1992) noted that many piscivorous birds, the definitive hosts of the main parasites of roach, gudgeon (*Ligula*) and pollan, occur inshore in L. Neagh while few piscivorous fish occur in the lough. Hence the inshore habitat in Lough Neagh has a higher reward rate for fish but also potentially more predators than offshore (though this is not relevant if *I. erraticus* transmission occurs mainly via fish scavenged from the shore). Hence the occurrence of more heavily parasitized pollan further offshore does not support the parasite manipulation hypothesis but is consistent with the reduced fitness/competition and infection risk hypotheses.

Costs of parasitism in pollan

Pollan were also infected, less frequently, by the intestinal cestode *Proteocephalus exiguus* (45% prevalence) and the ectoparasitic copepod *Argulus foliaceus* (0.3% prevalence) but infection intensity by these parasites was far less than by *Ichthyocotylurus* and

consequently we have assumed that the latter had the major impacts.

Petrushevski and Shulman (1961) noted that coregonids infected with *Tetracotyle* (a synonym of *Ichthyocotylurus*) showed severe reductions in condition. Dolezel and Crompton (2000) found that female *Coregonus lavaretus* in Loch Lomond were more heavily infected by *I. erraticus* than males, as in this study. In contrast to our results, they did not find any effect of parasitism on male condition but condition in parasitized females was reduced. They found that parasitism increased the gonadosomatic index in males but decreased it in female fish. Parasitism by *I. erraticus* also affects the pollan sexes differently.

In male pollan somatic condition, relative liver size and gonad size (Harrod and Griffiths, 2005) all decline with increasing infection intensity. The hepatosomatic index i.e. liver size relative to body mass is generally interpreted as an indicator of health since larger livers have greater energy reserves (Chellappa *et al.* 1995); the decreased liver mass in heavily parasitized pollan is consistent with this and the generally negative effect of parasitism on males. Parasitized females, despite being more heavily infected than males, show mixed responses to *I. erraticus*: somatic condition increased and there was no change in liver size, but gonad mass declined and gonads became asymmetric (Harrod and Griffiths, 2005).

Pulkkinen and Valtonen (1999) have shown that *C. lavaretus* infected by *Triaenophorus crassus* grew faster than uninfected fish until age 2 but subsequently grew more slowly: they postulated that parasitism increased food intake. However, parasitism did not affect pollan growth rates and heavily infected fish had lighter stomachs plus contents than lightly infected fish. It is not clear why larger fish of a given age were more likely to be infected.

A number of authors have shown that migration of *I. erraticus* cercariae through the host can cause significant tissue damage (Johnson, 1971; Swennen *et al.* 1979; Orecka-Grabda, 1991; Dolezel and Crompton, 2000). The metabolic demands of encysted metacercariae are probably small but mechanical effects are likely because of the space occupied by the cysts in the pericardium. Tort, Watson and Priede (1987) demonstrated that hearts of rainbow trout infected with metacercariae of *Apatemon gracilis* had stroke volumes approximately half those of uninfected fish, an effect that was subsequently attributed to constrictive pericarditis (Watson, Pike and Priede, 1992).

Shaw and Dobson (1995) suggested that there were evolutionary constraints on the degree of aggregation shown by parasites, only those with low pathogenicity being able to generate high infection intensities and a high level of aggregation. Infection

intensities of 600+ metacercariae, a mean variance:mean ratio of 249 and the apparently limited effects of *I. erraticus* on survival are consistent with this notion. Pollan is a glacial relict living in an unstratified lake (Harrod *et al.* 2002) that has become hypertrophic over the last 50 years (Wood and Smith, 1993). Low lake oxygen concentrations in August (Carter and Griffiths, 2001), coupled with increased oxygen requirements and perhaps thermal stress in warm summers, and reduced blood circulation due to parasitism now have the potential to affect pollan survival. Experimental evidence investigating the effect of *I. erraticus* infections on heart pumping and oxygen circulatory efficiencies would help to support this interpretation.

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