

Behaviour of roach (*Rutilus rutilus* L.) altered by *Ligula intestinalis* (Cestoda: Pseudophyllidea): a field demonstration

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SUMMARY

1. We studied the influence of a cestode parasite, the tapeworm *Ligula intestinalis* (L.) on roach (*Rutilus rutilus* L.) spatial occupancy in a French reservoir (Lake Pareloup, South-west of France).
2. Fish host age, habitat use and parasite occurrence and abundance were determined during a 1 year cycle using monthly gill-net catches. Multivariate analysis [generalized linear models (GLIM)], revealed significant relationships ($P < 0.05$) between roach age, its spatial occupancy and parasite occurrence and abundance.
3. Three-year-old roach were found to be heavily parasitized and their location toward the bank was significantly linked to parasite occurrence and abundance. Parasitized fish, considering both parasite occurrence and abundance, tended to occur close to the bank between July and December. On the contrary, between January and June no significant relationship was found.
4. These behavioural changes induced by the parasite may increase piscivorous bird encounter rate and predation efficiency on parasitized roach and therefore facilitate completion of the parasite's life cycle.

Keywords: host behaviour, *Ligula intestinalis*, parasite-mediated manipulation, parasitism, *Rutilus rutilus*

Introduction

Many trophically transmitted parasites alter their intermediate host's behaviour, mobility or motivation and facilitate continuation of their life cycle by way of predation (Holmes & Bethel, 1972; Moore, 1984, 1995; Dobson, 1988; Milinski, 1990; Moore & Gotelli, 1990; Poulin, 1994, 1995). Parasite-induced alterations in host behaviour are of potential importance for ecosystem functioning (Hurd, 1990; Combes, 1991; Thomas & Poulin, 1998; Poulin, Hecker & Thomas, 1998). Recently, Lafferty (1999) defined the phenom-

enon 'Parasite Increased Trophic Transmission (PITT)' which results from an evolutionary process that increases parasite fitness. For example, Giles (1987), showed that under laboratory conditions the metabolic respiratory demand of a parasitic tapeworm larva (*Schistocephalus solidus* L.) modifies the behaviour of its fish host, the stickleback (*Gasterosteus aculeatus* L.), and increases the encounter rate with ichthyophagous birds, the definitive host in the parasite's life cycle. Such host behaviour modification may represent a sophisticated product of parasite evolution aimed at host manipulation to facilitate transmission to the definitive host, rather than an accidental side-effect of infection (Barnard & Behnke, 1990). However, most research efforts on host-parasite systems have been conducted under highly unnatural laboratory conditions.

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Our study aims to test whether *Ligula intestinalis*, a widespread parasite of European Cyprinids, induces host behaviour modification under natural conditions. The life-cycle of *L. intestinalis* provides a convenient system to examine such questions. The tapeworm requires three distinct hosts to complete its life-cycle. The coracidium larva penetrates the gut wall of a copepod and develops into a proceroid. The infected copepod is ingested by a planktivorous cyprinid fish (e.g. roach *Rutilus rutilus* L.), and the parasite larvae develop into the plerocercoid stage in the body cavity. The definitive host is an ichthyophagous predatory bird in which *L. intestinalis* reaches sexual maturity. Parasite eggs are then released into the water with bird faeces. This parasite is known to induce severe pathological effects on fish (Van Dobben, 1952; Dence, 1958; Orr, 1966; Wilson, 1971; Holmes & Bethel, 1972; Harris & Wheeler, 1974; Sweeting, 1976; Arme, Bridges & Hoole, 1983; Taylor & Hoole, 1989).

We investigated the dynamics of host-parasite interactions from ingestion by the fish of the larvae to plerocercoid maturity in the fish, focusing on fish age and seasonal dynamics of horizontal roach distribution. Our results are used to test the PITT hypothesis in a natural environment.

Methods

Study site and sampling design

Lake Pareloup, a large oligo-mesotrophic reservoir (1260 ha, $168 \times 10^6 \text{ m}^3$), was selected as our study site. It is located in the South-west of France at an altitude of about 800 m, near the city of Rodez. Its maximum depth is 37 m, and mean depth 12.5 m. Lake Pareloup is a warm monomictic lake, with summer stratification and low oxygen concentration below the thermocline (located at about 10 m depth from early June to mid-September). The mean annual surface water temperature is 9 °C (range between 2 °C in February and 22 °C in July).

The selected intermediate fish host was the roach which is the main cyprinid species in lake Pareloup (Richeux *et al.*, 1994b). Monthly overnight gill-net roach samples were obtained from January to December 1998 (total of 583 specimens of fish). We used 30 m \times 1.7 m clear nylon monofilament gill-nets with different mesh openings (10, 14, 18, 20, 22 and 25 mm) to capture all roach sizes. Net height was sufficient to

cover almost the entire sampled area (i.e. from the lake bottom to the surface). The fish were sorted according to their location from the shore: 0–10, 10–20 and 20–30 m. We analysed variations in occurrence (presence/absence) and abundance (number of individuals per fish) of the parasite. All fish were dissected to collect the parasites. Plerocercoid larvae present in the abdominal cavity were counted. The fish were aged using scale measurements as described by Angelibert *et al.* (1999) for the roach population of lake Pareloup. The scales were cleaned in a 5% KOH solution before the adherent tissues were rubbed off with a soft brush. They were then rinsed in water and mounted on microscope slides for viewing on a microfiche viewer. The fish were grouped in four age classes: less than 2 years ($< 2^+$), 2 years (2^+), 3 years (3^+) and older than 3 years ($> 3^+$).

Statistical analyses

Generalized linear models (GLIM) (Wilson & Grenfell, 1997) were used to assess which explanatory variables and/or interaction terms best explained (i) parasite occurrence, (ii) parasite abundance, and (iii) fish abundance in relation to the distance from the bank. The variability in parasitic worm occurrence across roach individuals was studied using logistic regression (McCullagh & Nelder, 1989; Norusis, 1993). An analysis of deviance procedure with the sequential addition of the different predictor variables and their interactions was used to quantify the influence of each parameter. Differences between models were tested with chi-square statistics. When the order of entry of the different retained variables altered residual deviances and partial testing, we chose to arrange variables according to their Akaike information criterion from the lowest to the highest, using C_p statistics (see S-Plus 2000 Professional Release 2, 1999, MathSoft, Inc., New York, NY, U.S.A.). The C_p statistics was used to check for highly nested models (Venables & Ripley, 1994). To estimate the development of parasite abundance across host specimens, we used a GLIM model with a Poisson error and a log-link function which represented the most appropriate statistical tool (see Crawley, 1993 for more details). Chi-square and C_p statistics were used to evaluate differences between models.

The relative position of fish was tested using a GLIM model with a γ error and an inverse link

function. We compared the results obtained with the GLIM approach with traditional linear methods. The three variables, namely distance from the bank, fish age and season, were considered as continuous parameters in the GLIM model. Comparisons among medians were carried out using Kruskal–Wallis' statistics (Zar, 1996). We used the S-plus statistical package (Venables & Ripley, 1994) for calculations.

Results

Plerocercoid larva occurrence and abundance

Roach infected with plerocercoid larvae of *L. intestinalis* occupied very different localities in Lake Pareloup in comparison with uninfected fish. Greater parasite occurrence and abundance were observed closer to the inshore areas of the lake between July and December of 1998 (Figs 1 & 2) with number of plerocercoids per host ranging between 0 and 11 in

inshore areas (0–10 m), between 0 and 6 in the 10–20 m zone and between 0 and 3 in offshore areas (20–30 m). Season accounted for most of the total deviance in occurrence and abundance (47.7 and 64.6%, respectively). Distance explained around 13.2% of parasitized fish occurrence and 20.2% of parasite abundance. The direct effect of fish age was not significant ($P > 0.05$) for either occurrence or abundance, showing that parasite presence is not significantly linked with fish age (Tables 1 & 2). The interaction between season and fish age was highly significant in explaining occurrence (29.4%) and abundance (6%) of *L. intestinalis*, simply indicating that individual fish grow with time. In the same way, the season \times distance interaction was highly significant in explaining parasite abundance and accounted for about 5% of the total deviance, but was not significant ($P > 0.05$) in the case of parasite occurrence. This shows that fish are more heavily parasitized close to the bank, as visualized in Figs 1 & 2.

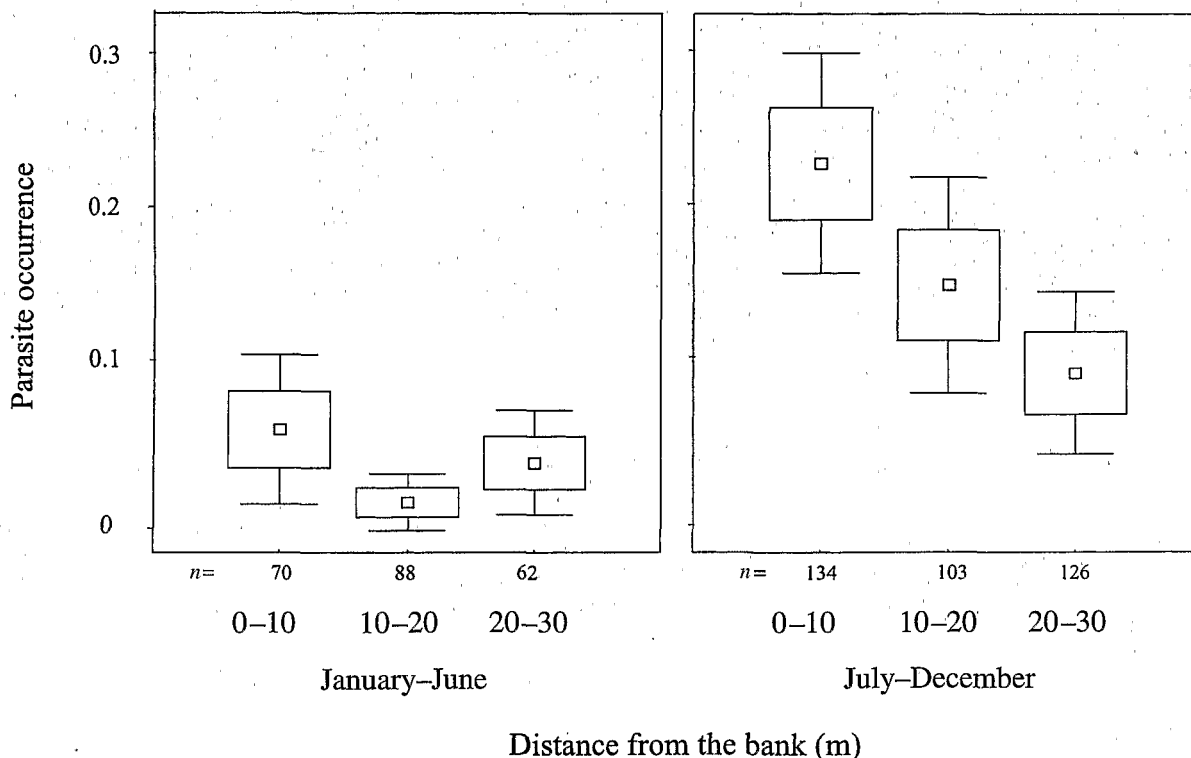


Fig. 1 Relationships between occurrence of *L. intestinalis* plerocercoid larvae in roach and distance from the bank during January–June and July–December. For clarity, monthly data were pooled in two half-year periods: winter and spring (from January to June), and summer and autumn (from July to December). The top, mid-line and bottom of each box plot represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles.

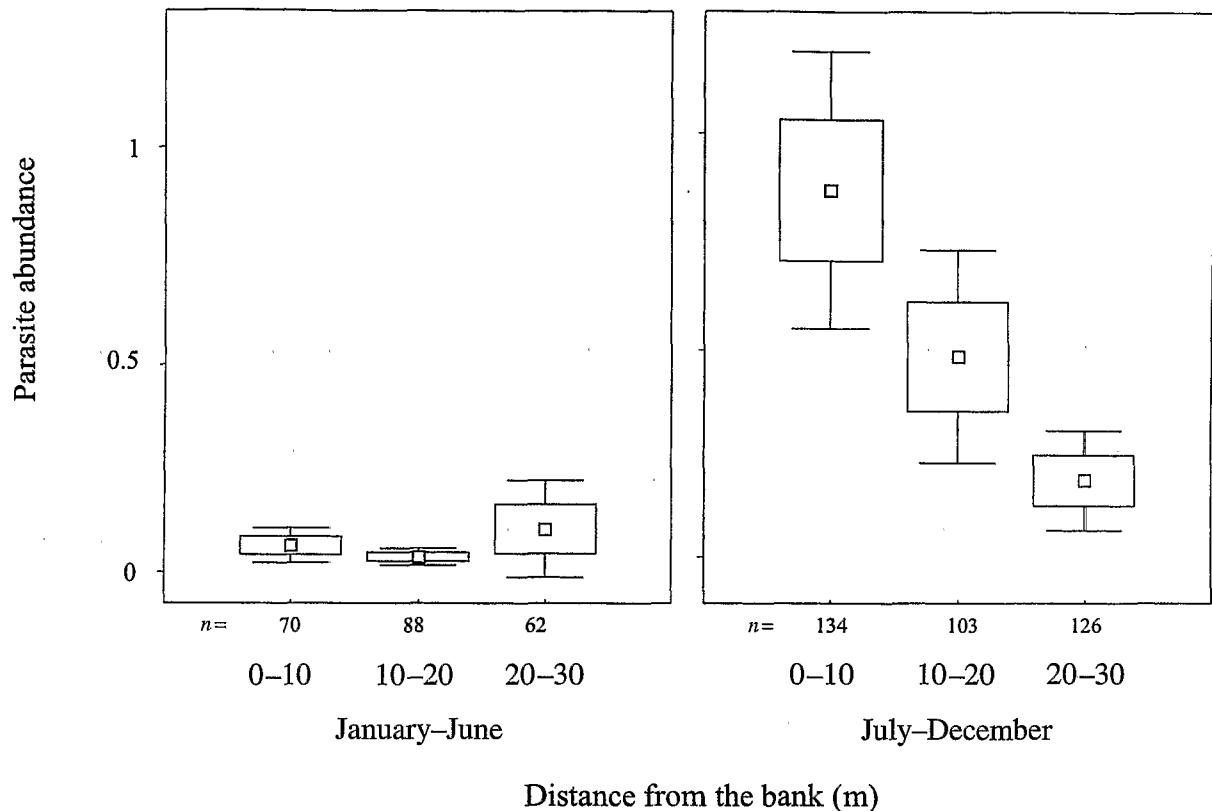


Fig. 2 Relationships between abundance of *L. intestinalis* larvae in roach and distance from the bank during January–June and July–December. For clarity monthly data were pooled in two half-year periods: winter and spring (from January to June), and summer and autumn (from July to December). The top, mid-line and bottom of each box plot represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles.

Table 1 Analysis of deviance table testing for effect of season, distance and fish age predictors and their two-way and three-way interaction terms on the level of parasite occurrence across fish host specimens using a binomial error and a logit link

	Deviance	d.f.	$P(\chi)$
Null	418.129	607	–
Season	32.951	1	< 0.0001
Distance	9.128	1	0.0025
Fish age	3.573	1	0.0587
Season × distance	0.246	1	0.6203
Season × fish age	20.347	1	< 0.0001
Distance × fish age	2.819	1	0.0931
Season × distance × fish age	0.063	1	0.8023

Table 2 Analysis of deviance table testing for effect of season, distance and fish age predictors and their two-way and three-way interaction terms on the level of parasite abundance across fish host specimens using a Poisson error and a log link

	Deviance	d.f.	$P(\chi)$
Null	905.929	607	–
Season	146.216	1	< 0.0001
Distance	45.642	1	< 0.0001
Fish age	0.772	1	0.3797
Season × distance	11.274	1	0.0008
Season × fish age	13.549	1	0.0002
Distance × fish age	4.157	1	0.0415
Season × distance × fish age	4.649	1	0.0311

Fish position

The study of fish position showed that parasite occurrence (Table 3) and abundance (Table 4) were both highly significant in accounting for variation in fish host position. Parasite occurrence and abundance

accounted for 40.7 and 50.5% of the deviance, respectively. The interaction terms season × fish age (18.6% for occurrence and 13.06% for abundance, Tables 3 & 4), season × parasite occurrence × fish age (20.1%, Table 3) and season × parasite abundance × fish age (20.2%, Table 4) also accounted for some of

Table 3 Analysis of deviance table testing for effect of season, parasite occurrence and fish age predictors and their two-way and three-way interaction terms on the position of fish individuals using a γ error and an inverse link (a model with a Poisson error yielded similar results for the same group of significant variables)

	Deviance	d.f.	P (F-ratio)
Null	663.782	610	–
Season	2.130	1	0.0832
Parasite occurrence	7.960	1	0.0008
Fish age	1.169	1	0.1992
Season \times parasite occurrence	0.704	1	0.3189
Season \times fish age	3.648	1	0.0235
Parasite occurrence \times fish age	0.008	1	0.9175
Season \times parasite occurrence \times fish age	3.941	1	0.0186

Table 4 Analysis of deviance table testing for effect of season, parasite abundance and fish age predictors and their two-way and three-way interaction terms on the position of fish individuals using a γ error and an inverse link (a model with a Poisson error yielded similar results for the same group of significant variables)

	Deviance	d.f.	P (F-ratio)
Null	657.917	607	–
Season	2.267	1	0.0768
Parasite abundance	15.697	1	< 0.0001
Fish age	1.328	1	0.1754
Season \times parasite abundance	6.283	1	0.0033
Season \times fish age	4.054	1	0.0181
Parasite abundance \times fish age	0.064	1	0.7655
Season \times parasite abundance \times fish age	1.360	1	0.1703

the total deviance in the models. Comparison of frequency distributions of uninfected and infected fish specimens across all age classes showed significant differences (Pearson $\chi^2 = 32.222$, d.f. = 3, $P < 0.0001$, maximum likelihood $\chi^2 = 31.543$, d.f. = 3, $P < 0.0001$) with 3-year-old individuals responsible for most of the observed difference (Pearson $\chi^2 = 30.571$, d.f. = 1, $P < 0.0001$, maximum likelihood $\chi^2 = 27.061$, d.f. = 1, $P < 0.0001$).

Season- and age-dependency of host infestation

A temporal difference in parasitism was found in both parasite occurrence (Kruskal–Wallis $\chi^2 = 98.773$, d.f. = 11, $P < 0.0001$) and abundance ($\chi^2 = 99.558$, d.f. = 11, $P < 0.0001$). Fish individuals showed significantly higher levels of parasite occurrence ($\chi^2 = 16.347$, d.f. = 1, $P = 0.0001$) and parasite abundance ($\chi^2 = 17.913$, d.f. = 1, $P < 0.00005$) in October than in other months. This was also verified between November and other months for both parasite occurrence ($\chi^2 = 10.555$, d.f. = 1, $P = 0.0012$) and abundance ($\chi^2 = 9.757$, d.f. = 1, $P = 0.0018$).

Concerning the relationship between parasitism and fish age, we observed differences in parasite occurrence ($\chi^2 = 39.418$, d.f. = 3, $P < 0.0001$) and abundance ($\chi^2 = 39.733$, d.f. = 3, $P < 0.0001$) across the four fish age classes (see Figs 3 & 4, respectively).

Three-year-old fish (middle age class) had significantly higher parasite occurrence ($\chi^2 = 31.265$, d.f. = 1, $P < 0.00005$) and abundance ($\chi^2 = 28.647$, d.f. = 1, $P < 0.00005$) than the other age classes. In other months, during October and November the most heavily infected fish were 3-year-old roach which were preferentially located in the inshore areas.

Discussion

Host–parasite interactions between cestodes and fish have rarely been investigated in natural environments. Our findings concerning littoral migration of parasitized roach can be considered complementary to the experimental laboratory studies of Lester (1971) and Giles (1983, 1987) who revealed the physiological causality of the vertical migration of parasitized sticklebacks. The relationship in our study between host age and parasite occurrence and abundance can be interpreted in terms of density-dependent host mortality, as described by Anderson & Gordon (1982). The decrease in parasite occurrence and abundance in fish older than 3 years is the result of mortality induced by the parasite. As far as 3-year-old fish are concerned, several hypotheses can be formulated to explain the differential spatial distribution of parasitized and non-parasitized individuals.

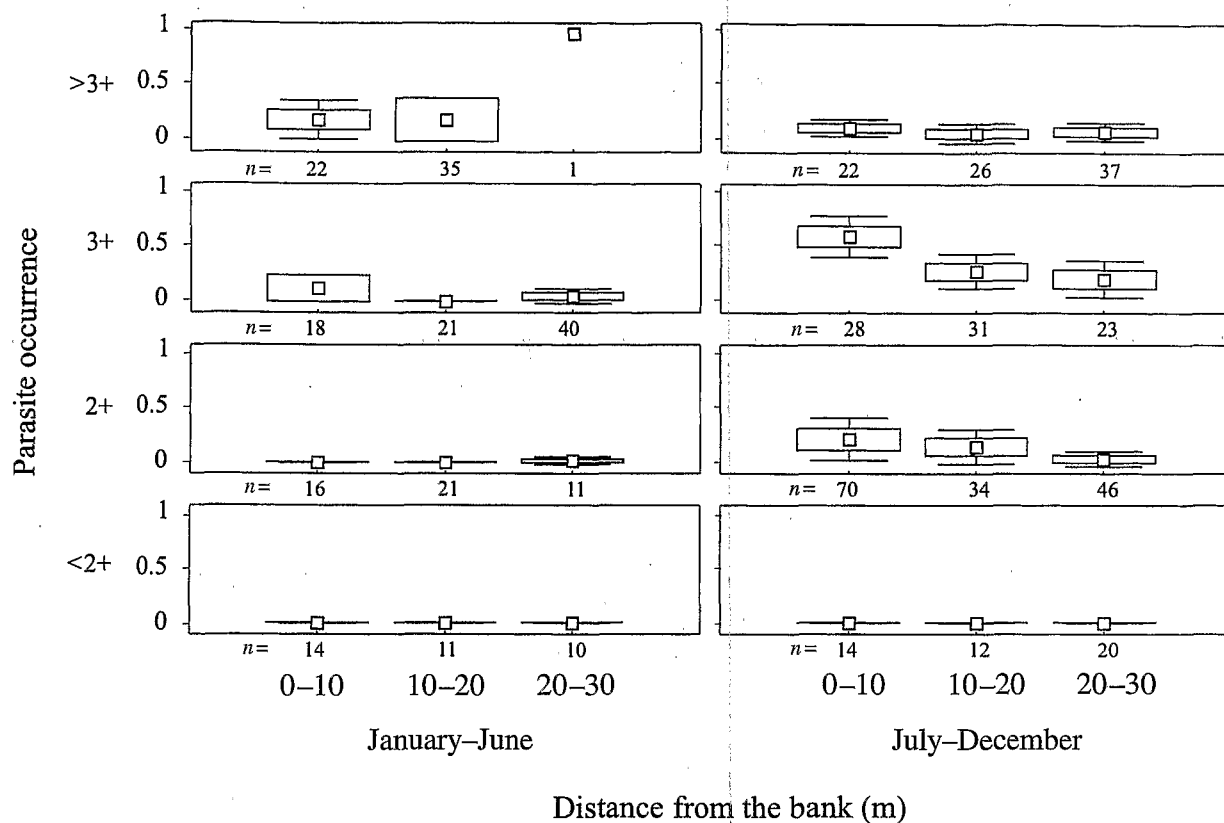


Fig. 3 Relationships between occurrence of *L. intestinalis* plerocercoid larvae in four age classes of roach (<2 years, 2 years (2+), 3 years (3+) and older than 3 years) and distance from the bank during January–June and July–December. For clarity monthly data were pooled in two half-year periods: winter and spring (from January to June), and summer and autumn (from July to December). The top, mid-line and bottom of each box plot represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles.

The hypothesis that fish are more exposed to parasite infection in littoral areas because of a possible horizontal gradient of parasitized copepod (the previous host in the *L. intestinalis* life cycle) cannot be excluded. However, intermediate host copepod species (*Cyclops vicinus vicinus* and *Acanthocyclops robustus*) do not exhibit any differential abundance within the study site (between the bank and 30 m offshore, i.e. the area sampled by the gill-nets). Similarly, no spatial heterogeneity in copepod infection rate by *L. intestinalis* was observed during the study. Therefore, the hypothesis of differential fish infection rate within the study site is not supported.

The relationships between fish spatial distribution and parasitism in Lake Pareloup suggests the existence of a behavioural manipulation of roach by *L. intestinalis*. This allows several potential explanations, ranging from purely accidental to a variety of adaptive scenarios.

One might hypothesize that host migration simply corresponds to an accidental side-effect of infection. As Williams, MacKenzie & McCarthy (1992) warn, complex biological systems can create numerous incidental effects that are not necessarily adaptive. Thus, lower activity levels in more heavily infected fish could lead to their accumulation in littoral areas of Lake Pareloup where they find more appropriate conditions for survival in terms of prey abundance.

Although we cannot reject this hypothesis, both the debilitating effects exerted by *L. intestinalis* on hosts (Van Dobben, 1952; Dence, 1958; Orr, 1966; Wilson, 1971; Holmes & Bethel, 1972; Harris & Wheeler, 1974; Sweeting, 1976) and the complexity of *L. intestinalis* life cycle (with several defined hosts necessary to complete life cycle) suggest that behavioural changes are parasite-oriented as an adaptation to increased energy demands. Thus, during autumn, *L. intestinalis* grows markedly in the host body cavity, and

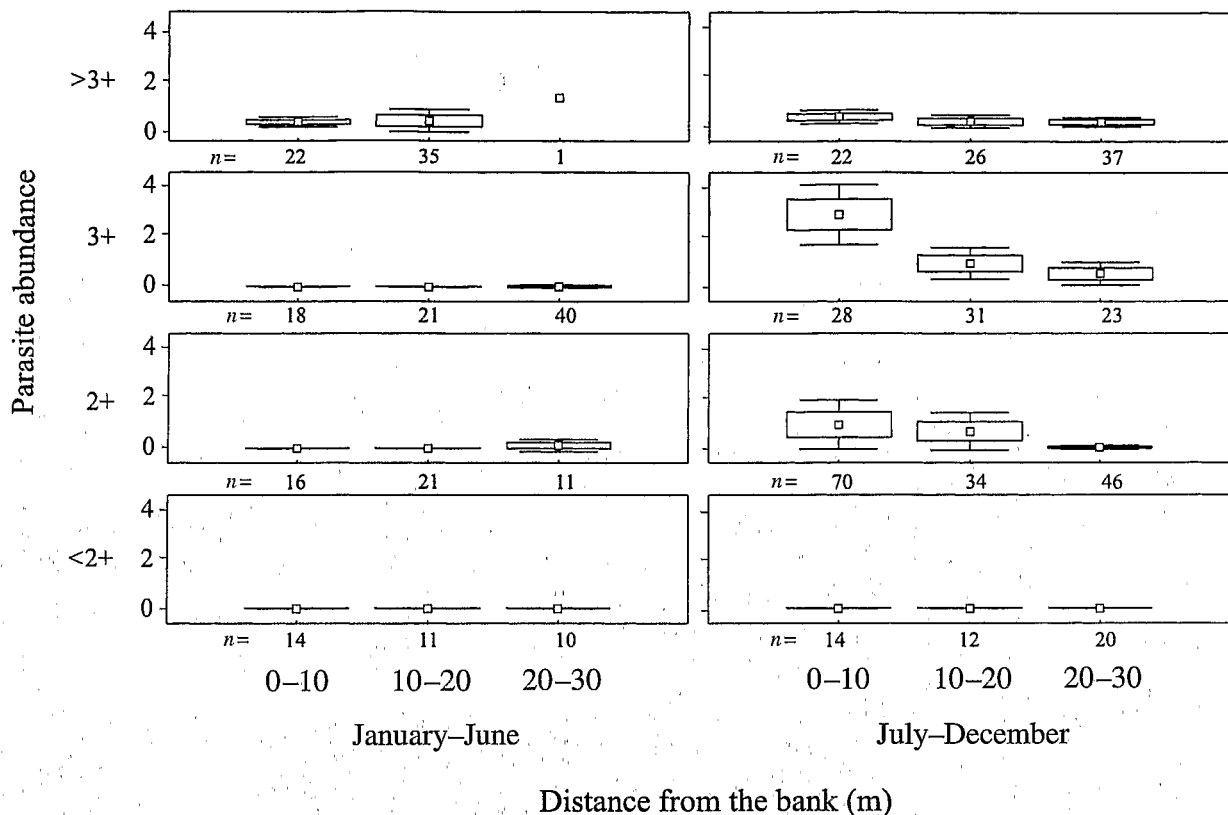


Fig. 4 Relationships between parasite abundance of *L. intestinalis* plerocercoid larvae in four age classes of roach (< 2 years, 2 years (2+), 3 years (3+) and older than 3 years) and distance from the bank during January–June and July–December. For clarity monthly data were pooled in two half-year periods: winter and spring (from January to June), and summer and autumn (from July to December). The top, mid-line and bottom of each box plot represent the 75th, 50th and 25th percentiles, respectively; the horizontal lines represent the 10th and 90th percentiles.

plerocercoids may reach a size between 10 and 30 cm long (Arme & Owen, 1968), placing a considerable demand on the energy reserves of its host. Consequently, *L. intestinalis* stimulates host foraging behaviour by increasing feeding motivation, as maintained by Pascoe & Matthey (1977), Giles (1983), Milinski (1985) and Godin & Sproul (1988). However, because of the pathogenic effects of the parasite, the competitive ability of roach is reduced (e.g. lowered swimming efficiency). This could explain the exclusive occupation by heavily parasitized roach of the productive littoral areas of the lake (Fisher & Eckmann, 1997), whereas non-parasitized fish are mainly located in less productive but safer areas between 10 and 30 m from the bank, in accordance with the so-called trade-off between costs and benefits (Persson & Eklov, 1995; Begon, Harper & Townsend, 1996).

Alteration in host behaviour by *L. intestinalis* is probably to favour processes oriented towards

selective predation by ichthyophagous birds. Indeed, predator encounter rates with species like yellow-legged gulls (*Larus cachinnans* L.), black-headed gulls (*Larus ridibundus* L.), cormorants (*Phalacrocorax carbo* L.) and grey herons (*Ardea cinerea* L.) are increased because these birds characteristically occupy the lake during autumn and exhibit maximal predation efficiency in littoral waters (Bousquet, 1992; Joachim, Bousquet & Faure, 1997). Moreover, previous studies on Lake Pareloup revealed that pike (*Esox lucius* L.) mainly exploit offshore waters during this period (Brosse, 1999), reducing predation on heavily infected roach by unsuitable fish predators (i.e. those which do not constitute a host for the parasite). As a consequence, our results are in accordance with the PITT hypothesis (Lafferty, 1999); infected roach movement close to the shore can be considered to maximize the likelihood of life cycle completion by *L. intestinalis*.

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