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Parasite-induced mortality in three host populations of the roach *Rutilus rutilus* (L.) by the tapeworm *Ligula intestinalis* (L.)

G. Loot[1, 2]
S. Lek[1]
D. Dejean[1]
J.F. Guégan[3]

Keywords : *Rutilus rutilus, Ligula intestinalis*, parasitism, aggregation, host mortality.

Patterns of parasite infestation by plerocercoid forms of the tapeworm *Ligula intestinalis* (Cestoda, Pseudophyllidea) in the second intermediate host, the roach *Rutilus rutilus*, were analysed in three fish populations of South-Western France during 1998. In all three studied sites, *i.e.* Pareloup Lake, Lavernose-Lacasse and Muret gravel pits, roach were commonly parasitized with plerocercoids. A strong increase in prevalence, mean number of parasites and parasitic load was observed in the youngest hosts with a maximum peak reached in the medium-age (2+, 3+)roach classes. Such trends as a function of host fish age would indicate the occurrence of parasite-induced host mortality, with the most heavily infected fish specimens being removed from the three roach populations. The three roach populations infected by *L. intestinalis* exhibit different patterns of parasite-induced mortality which could correspond to different possible ecological and evolutionary responses associated with local variation in host-parasite interactions. The parasite-induced host mortality observed, *i.e.* direct mortality caused by pathogenic effects and /or enhanced fish predation by piscivorous birds to increase parasitic transmission is discussed within the context of the adaptative parasite-induced manipulation hypothesis.

Mortalité induite dans trois populations de gardons hôtes *Rutilus rutilus* (L.) par le parasite *Ligula intestinalis* (L.)

Mots clés : *Rutilus rutilus, Ligula intestinalis*, parasitisme, agrégation, mortalité.

La relation entre le taux d'infestation des gardons *Rutilus rutilus* par des larves plérocercoïdes de la ligule, *Ligula intestinalis* (Cestoda, Pseudophyllidea) et l'âge de ces gardons hôtes a été étudiée au cours de l'année 1988 dans trois populations du Sud-Ouest de la France. Selon les trois sites étudiés, le lac de Pareloup et les gravières de Lavernose-Lacasse et Muret, les gardons sont parasités à différents degrés d'infestation. Une augmentation de la prévalence, de l'abondance moyenne en larves plérocercoïdes et de la charge parasitaire totale est mise en évidence chez les plus jeunes gardons ; elle correspond à une accumulation des formes parasitaires. Pour les trois sites étudiés, le parasitisme par la ligule atteint son maximum d'infestation chez le gardon dans les classes d'âge moyennes (2+, 3+) et diminue ensuite dans les classes d'âge plus anciennes (4+, 5+, 6+). Ces évolutions de la prévalence parasitaire, de l'abondance moyenne et de la charge parasitaire en fonction de l'âge de l'hôte sont compatibles avec l'hypothèse d'une mortalité des poissons hôtes ; les gardons les plus âgés et les plus parasités disparaissant de la population. Les courbes de mortalité des gardons diffèrent chez les trois populations étudiées. Ce résultat suggère l'existence de réponses écologiques et évolutives distinctes entres les trois associations locales hôtes-parasites. Les mortalités différentielles entre les populations de gardons parasités causées soit par une mortalité directe, soit par une mortalité par prédation, sont discutées dans le contexte de l'hypothèse d'une modification du comportement de l'hôte par le parasite.

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1. Centre d' Ecologie des Systèmes Aquatiques Continentaux, UMR C5576 CNRS, Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse Cedex 04, France.
2. Corresponding author : E-mail: loot@cict.fr
3. Centre d'Etudes sur le Polymorphisme des Micro-organismes, Centre I.R.D. de Montpellier, U.M.R. 9926 C.N.R.S.-I.R.D., 911 avenue du Val de Montferrand, F-34032 Montpellier Cedex, France.

1. Introduction

The study of parasite-induced alterations in host behaviour, or coloration, has received much attention during the last decade (see Combes 1991, Clayton & Moore 1997, Poulin 1998 a for reviews). Parasites may directly affect their hosts through pathological effects, or through host phenotypic modification, which could benefit either the host or the parasite (Poulin 1998 b). Parasites with a complex life-cycle, may alter the behaviour of intermediate hosts which represents a subtle strategy for parasites to achieve their goal, and thus to increase their fitness. Among parasites, the nematodes and cestodes are probably the two groups able to alter host activity (Poulin 1994). For instance, the tapeworm, *Ligula intestinalis*, which has a complex life-cycle with three distinct hosts necessary for its complete development, increases the vulnerability of its intermediate fish host to predation by piscivorous birds by altering fish behaviour and by the severe pathological effects it can inflict (Van Dobben 1952, Wilson 1971, Holmes & Bethel 1972, Harris & Wheeler 1974, Sweeting 1976). In addition, these pseudophyllidean tapeworm systems are remarkable in that the effects of plerocercoid infections may considerably modify host phenotypes. Plerocercoids divert energy away from host reproduction towards their own growth that preventing the sexual development of the fish (Walkey & Meakin 1970, Kuris 1974, Baudoin 1975, Poulin 1998a). They also produce growth hormones bearing some similarity to human growth hormones, which induce a number of effects such as lipogenesis (Phares 1997).

Even though many parasite taxa are known to modify their host phenotypes, relatively few studies have examined the evolutionary consequences of such parasite strategies on ecosystems. Recently, Thomas et al. (1999) suggested that some parasites are directly or indirectly involved in engineering processes through the phenotypic alterations they could induce in their hosts. Little is known about the exact role played by parasites in these processes and this is mainly due to the lack of field information on *i* the relative importance of such parasites in ecosystems, *ii* their regulatory impact on host populations, and *iii* their effects on predator behaviour.

As recently pointed out by Kuris (1997), pseudophyllidean tapeworms provide an interesting opportunity to test some ideas on the evolution of trophic transmission by parasites with complex life-cycles.

Here, we compare the effects of the helminth tapeworm, *Ligula intestinalis*, in three distinct fish populations of the roach, *Rutilus rutilus*. We try to quantify the impact exerted by these parasites on their host populations. Since host-parasite interactions produce different outcomes in different environments, we may expect that distinct fish populations are differently affected by *Ligula intestinalis*. Finally, we discuss the magnitude of the parasite infestation observed in fish hosts and its cost for intermediate hosts within the context of the adaptative PITT- Parasite Increases Trophic Transmission strategy- (Lafferty 1999).

2. Material and methods

2.1. Study sites

Three sites from South-West France were surveyed during 1998, *i.e.* Lavernose gravel pit, Muret gravel pit and Pareloup lake (Fig. 1).

- The Lavernose gravel pit, near the city of Toulouse, is situated on the alluvial plain of the Garonne River, the fourth largest river in France (Fig. 1). This eutrophic gravel pit is 190 m above sea level, its surface area is 23 ha with a maximum depth of about 4 m, and a mean depth of around 2 m. The average annual water temperature is around 14 °C (range 5-25 °C).

- The Muret gravel pit is also near Toulouse, and belongs to the alluvial plain of the Garonne River (Fig. 1). This eutrophic gravel pit is 175 m above sea level, its surface area is 17 ha with a maximum depth of about 4 m, and a mean depth of around 2 m. The average annual water temperature is similar to that of the Lavernose gravel pit.

- The Pareloup lake, which is an oligo-mesotrophic lake, is the fifth largest hydroelectric reservoir in France (1260 ha, 168.10^6 m^3). This body of water is located near the city of Rodez (Fig. 1). It is 800 m above sea level, with a maximum depth of about 37 m and the majority of its floor lying below 12.5 m of water. The average annual water temperature is 9 °C (range 2-22 °C).

2.2. The parasite

Ligula intestinalis (Cestoda, Pseudophyllidea) shows a complex life-cycle (Rosen 1920) with three hosts necessary for its complete development. The first host is a copepod, in which the coracidium larva develops into a procercoid form. Then, the second host is a planktivorous fish in which the procercoid larva evolves into a plerocercoid larva located in the host abdominal cavity. Plerocercoids may cause severe impact on fish host viability and numerous studies have listed cases where this worm has been responsible for pathogenic effects in fish (Moisan 1956, Arme &

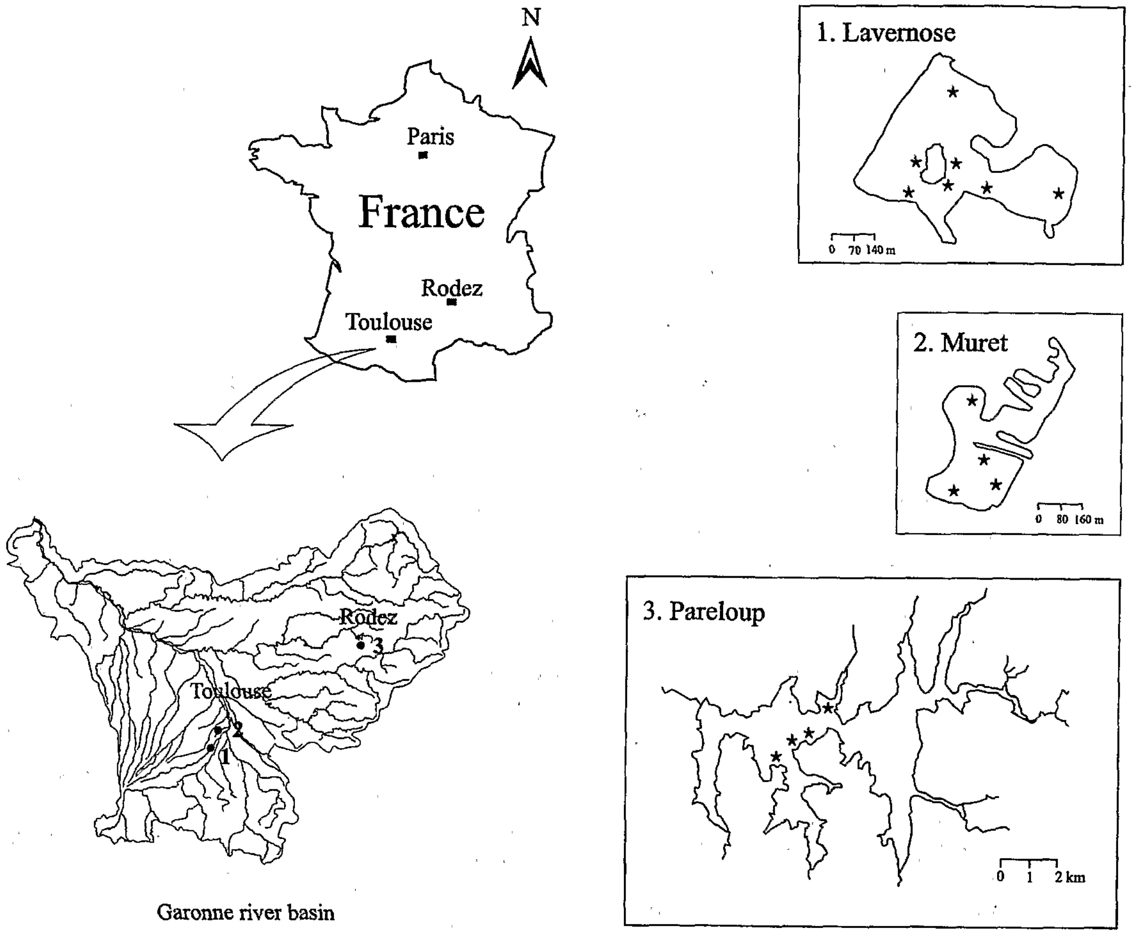

Fig.1. Geographical distribution of the three sites studied. Stars indicate sampling sites.

Fig.1. Distribution géographique des trois sites étudiés. Les étoiles indiquent les zones d'échantillonnage.

Owen 1968, 1970, Sweeting 1975, Wyatt & Kennedy 1989). The final host is an ichthyophagous bird. Birds commonly associated with parasite transmission are the Great Crested Grebes (*Podiceps cristatus*), yellow herring gulls (*Larus cachinnans*) and cormorants (*Phalacrocorax carbo*) (Dubinina 1980), species commonly present in the three studied sites.

2.3. Fish sampling

Samples of roach were collected during 1998 at the three sites, *i.e.* Pareloup lake (704 specimens), Lavernose gravel pit (773 specimens) and Muret gravel pit (489 specimens). Since fish samples may be biased by the catching technique, *e.g.* gill-nets even with the smallest mesh sizes are able to catch only sub-juvenile specimens, we decided to use an association of the different methods to sample all possible length classes of roach. In the littoral area where flooded vegetation is abundant, electrofishing was used whereas when flooded vegetation was absent or very scarce, we used a small seine-net. In open waters, these methods were simply inappropriate, and we used gill-nets (1.6 m high, 20 m long) made of clear nylon monofilaments. For this survey, different mesh sizes (10, 14, 18, 20, 22, 25 mm measured between adjacent knots) were used. Sampling techniques were sufficiently appropriate *i* to catch a wide range of fish sizes, and *ii* to collect fish specimens present in different habitats within the three sites.

2.4. Data

Just after their capture, all fish were measured to the nearest millimeter (total body length). Then, they were weighed to the nearest gram. We dissected each individual roach to count and weigh the plerocercoid larvae present in the abdominal cavity. We estimated the mean parasite abundance and the parasite load. The parasitic load of each fish when plerocercoids occurred was quantified using the Index of Parasitization (I.P.) of Kennedy & Burrough (1980). This index is calculated as the ratio of the total weight of plerocercoids per host to the total weight of the host minus the total weight of parasites, with this ratio then being multiplied by 100. For ageing purposes, 10-20 scales were detached from the area above the lateral line, on the left side of each fish. 4-8 scales were cleaned by soaking in a 5 % KOH solution before rubbing off the adherent tissues with a small brush. Then, they were rinsed with water and placed between slides for viewing on a microfiche viewer. Scale examination has long been known to be an efficient tool for fish ageing (Hartley 1947). For estimating the mortality due to parasites we used the method described by Lester (1984). Aiming to observe a decrease in the prevalence, mean parasite abundance (average number of parasite) and parasite load with host age.

2.5. Statistical analysis

Parasite accumulation through time increases the mean parasite abundance in older classes for parasites with low virulence because older hosts have been exposed to parasite infection for a longer period of time. When the host mortality rate may be possibly caused by a parasite intensity-dependent phenomenon, curves of mean parasite abundance versus host age are convex which is explained by the death of the most heavily infected hosts which are selectively removed from the population sampled. The curve for both prevalence and mean parasite abundance directly reflects the magnitude of parasite-induced host mortality with age. The mortality rate may be caused by a parasite-load-dependent phenomenon, curves of parasite index as a function of host age are convex. The maximum prevalence, mean parasite abundance and parasite load values correspond to the host age class (i.e. modal age class) subjected to the highest parasite impact.

Finally, in order to determine a change in degree of parasite infestation with host age, we used non-parametric statistics, *i.e.* Kruskall-Wallis' K statistics. Results were considered to be significant at the 5 % level. All analyses and statistical graphics were performed using SPSS release 8 for Windows, the Statistical Package for the Social Sciences (Norusis 1993).

3. Results

Commonly, the second intermediate host of *Ligula intestinalis* is a cyprinid fish. At Pareloup, the roach is the predominant species within the fish community (85.3 %) (Table1) ; it is known to spawn between end of May and beginning of June (Richeux et al. 1994). At Lavernose, the only two fish species make up almost the whole community : roach (44.4 %) and bream (54.6 %) (Table 1), with a roach spawning period occurring sooner than at Pareloup lake between the end of April and the beginning of May. At the Muret gravel-pit, the two most abundant fish species are the roach (30.6 %) and the crucian carp (48.5 %) (Table1), with a roach spawning period similar to that prevailing at Lavernose.

At Lavernose, Muret and Pareloup, the roach is heavily infected by the tapeworm. The frequency distribution of *Ligula intestinalis* plerocercoid specimens within their host individuals conforms to a negative binomial distribution for the lakes (Fig. 2). The normality test (Kolmogorov-Smirnov test) gives $P < 0.05$ for the three cases. The values of the aggregation coefficient k calculated using the non-linear maximum-likelihood method are 0.052, 0.350 and 0.268 with the mean plerocercoid number equaling 1.79 (s.d. = 3.19), 0.138 (s.d. = 0.63) and 0.440 (s.d. = 0.96) respectively for the three localities. All k parameters indicate that infrapopulations of plerocercoid forms are strongly clumped within their host with the highest levels of aggregation occurring at Lavernose.

Figure 3 illustrates changes in a) prevalence b) mean parasite abundance and c) mean parasite index (PI) with fish age for the three localities, Lavernose, Muret and Pareloup. Juveniles are weakly infected with plerocercoid forms, and the infection rate increases rapidly with host age. A maximum level of prevalence, mean parasite abundance and PI occurs in the medium-size individuals for the three host populations. The oldest individuals are weakly infected by parasite worms in the three sites. Trends in changes of parasite index with host size are strongly significant for the three sites, *i.e.* Lavernose (Kruskall-Wallis' test, $K = 236.352$, $d.f. = 7$, $p < 0.001$), Muret ($K = 15.140$, $d.f. = 7$, $p < 0.05$) and Pareloup ($K = 451.022$, $d.f. = 7$, $p < 0.001$), changes in mean parasite abundance are significant, *i.e* Lavernose (Kruskall-Wallis' test, $K = 125.149$, $d.f. = 6$, $p < 0.001$), Muret ($K = 20.99$, $d.f. = 6$, $p < 0.01$) and Pareloup ($K = 23.122$, $d.f. = 7$, $p < 0.01$). In addition, it is noticeable that the three roach populations show a somewhat asynchronous trend which may reflect differences between the three host

Table 1. Cyprinid fish abundance (%) in the three sites and parasite prevalence (%) for each fish species.

Table 1. Abondance (%) des poisssons Cyprinidés dans les trois sites et prévalence parasitaire (%) pour chaque espèce.

Site	Species		Abundance	Prevalence
1 Lavernose	Silver bream	*Blicca bjoerkna*	54.6	0
	Roach	*Rutilus rutilus*	44.4	32.2
	Carp	*Cyprinius carpio*	0.7	0
	Bleak	*Alburnus alburnus*	0.3	0
2 Muret	Crucian carp	*Carassius carassius*	48.5	0
	Roach	*Rutilus rutilus*	30.6	7.7
	Chub	*Leuciscus cephalus*	15.6	0
	Rudd	*Scardinius erythrophtalmus*	3	0
	Gudgeon	*Gobio gobio*	1.8	0
	Carp	*Cyprinius carpio*	1	0
3 Pareloup	Roach	*Rutilus rutilus*	85.38	9.3
	Rudd	*Scardinius erythrophthalmus*	9.45	0.5
	Common bream	*Abramis brama*	5	0
	Bleak	*Alburnus alburnus*	0.05	2.5
	Carp	*Cyprinius carpio*	0.04	0
	Gudgeon	*Gobio gobio*	0.04	1
	Chub	*Leuciscus cephalus*	0.03	0
	Tench	*Tinca tinca*	0.01	0

sites. The maximum parasite load and the average number of plerocercoid worms reaches respectively 7.8 ± 0.56 g and 2.85 ± 0.21 individuals for Lavernose, 0.93 ± 0.44 g and 0.32 ± 0.09 individuals for Muret and 2.77 ± 0.64 g and 0.43 ± 0.09 individuals for Pareloup which corresponds to distinct modal age classes, *i.e.* specific host age class where parasite induced mortality occurs (age 2 for Lavernose, age 3 for Muret and Pareloup). The maximum of prevalence reaches respectively 55 %, 11 % and 14 % for Lavernose, Muret and Pareloup. The roach of Lavernose population are heavily infected and *L. intestinalis* probably has a severe impact on the fish population.

Concomitant with the decline of mean parasite abundance and parasite load for the highest age classes, we observed for the three localities (Fig. 3a) a similar tendency in the behaviour of prevalence curves.

4. Discussion

Usually, free-living organisms in nature have a tendency to increase aggregation or, on the contrary, to exert repulsion between congeners (Taylor & Taylor 1977, Tokeshi 1999). Likewise, parasite forms are not evenly distributed among their hosts, and a large number of host individuals generally tend to harbour no or few parasites while very few hosts present numerous parasites (Anderson & Gordon 1982, Dobson & Merenlender 1991, Shaw & Dobson 1995, Wilson & Grenfell 1997). As illustrated in this study, the pseudophyllidean plerocercoids of *Ligula intestinalis*, which parasitize the roach as a second-intermediate host, show a similar trend toward clumped spatial and temporal distribution within their fish hosts. Few host individuals are heavily infected by plerocercoids with up to 17 plerocercoids found in the abdominal cavity of a single roach whereas many individuals are uninfected

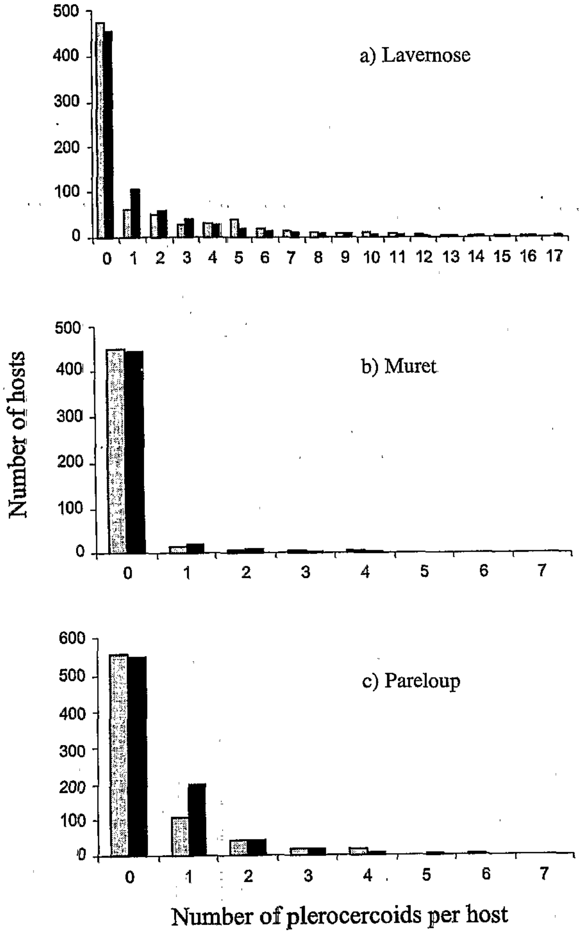

Fig.2. Frequency distribution of *Ligula intestinalis* in roach, *Rutilus rutilus*, compared to the negative binomial distribution across three host populations, *i.e.* a) Lavernose gravel-pit, b) Muret gravel-pit and c) lake Pareloup. Solid bars illustrate the observed frequency of plerocercoid worms and empty bars their estimated corresponding frequency using non-linear maximum likehoods.

Fig.2. Distribution de fréquence du nombre de ligules, *Ligula intestinalis*, par gardon, *Rutilus rutilus*, comparé avec une distribution binomiale négative pour les populations hôtes des sites étudiés : a) gravière de Lavernose, b) gravière de Muret, c) lac de Pareloup. Les histogrammes noirs représentent la fréquence observée des plérocercoïdes et les histogrammes blancs leur fréquence estimée à l'aide de la loi du maximum de vraisemblance.

or slightly affected by parasitic larval forms. Such parasite aggregations have often been found to affect host viability in natural populations. It is likely here that such heavily infected fish hosts are missing from the samples because of increased mortality, *i.e.* direct mortality caused by pathogenic effects and/or mortality caused by piscivorous birds predation.

Convex curves of prevalence, mean parasite abundance and parasite load within fish hosts demonstrate this disappearance of heavily infected hosts. Such curves obtained with host age might simply result from statistical artefacts when parasites affect host growth but not host viability (Rousset et al. 1996). This phenomenon is unlikely to happen for *L. intestinalis* since many investigations have demonstrated the severe impact exerted by this tapeworm on fish (Wilson 1971, Sweeting 1976, Burrough 1979, Kennedy & Burrough 1980, Wyatt & Kennedy 1989), and we have investigated a growth increase in roach infested with *Ligula* plerocercoids (Loot et al., unpublished data). Convex curves may be generated by age-related changes in average infection rate (Anderson & Gordon 1982). Older hosts may cease to acquire parasites as a consequence of immunity acquisition. In addition, such curves may also be obtained in the case of "prevalence-dependent" model of parasitism (Rousset et al. 1996). According to this model, host mortality rate does not increase with parasite abundance, but it simply depends on the presence or absence of a given parasite. Thus, successive infestations, as observed in multi-infected fish, have no further effect on host mortality (Bean & Winfield 1992). Our results demonstrate that *Ligula intestinalis* has detrimental effects on host viability through accumulation of plerocercoid forms whereas infections of single parasites do not necessarily induce strong direct pathogenic effects, lesions or atrophies.

Interestingly, the three infested roach populations differ in their degree of infection level, *i.e.* maximum prevalence, abundance and parasite load, and in intermediate host characteristics, *i.e.* modal age at which most heavily infected hosts are observed. The differences across sites would tend to indicate that host-parasite interactions produce different combinations of larval longevity, degree of maturity and spatial aggregation in hosts. Indeed, the Lavernose host population appears to be the most strongly affected by deleterious plerocercoid effects. Massive accumulation can occur in which the weight of total *L. intestinalis* specimens may equal, or even exceed, the weight of the host. Such situations are fatal for the intermediate fish hosts and lead to parasites losses. Aggregation thus reduces the deleterious effect of *L. intestinalis* specimens on fish populations and parasites participating in aggregations lose out on reproductive success (Jaenike 1996). In case of single or weakly infestation, pathogens effects are less severe and plerocercoid larvae will be less likely to be successfully transmitted because the host grows too large. Smaller fishes are more suscep-

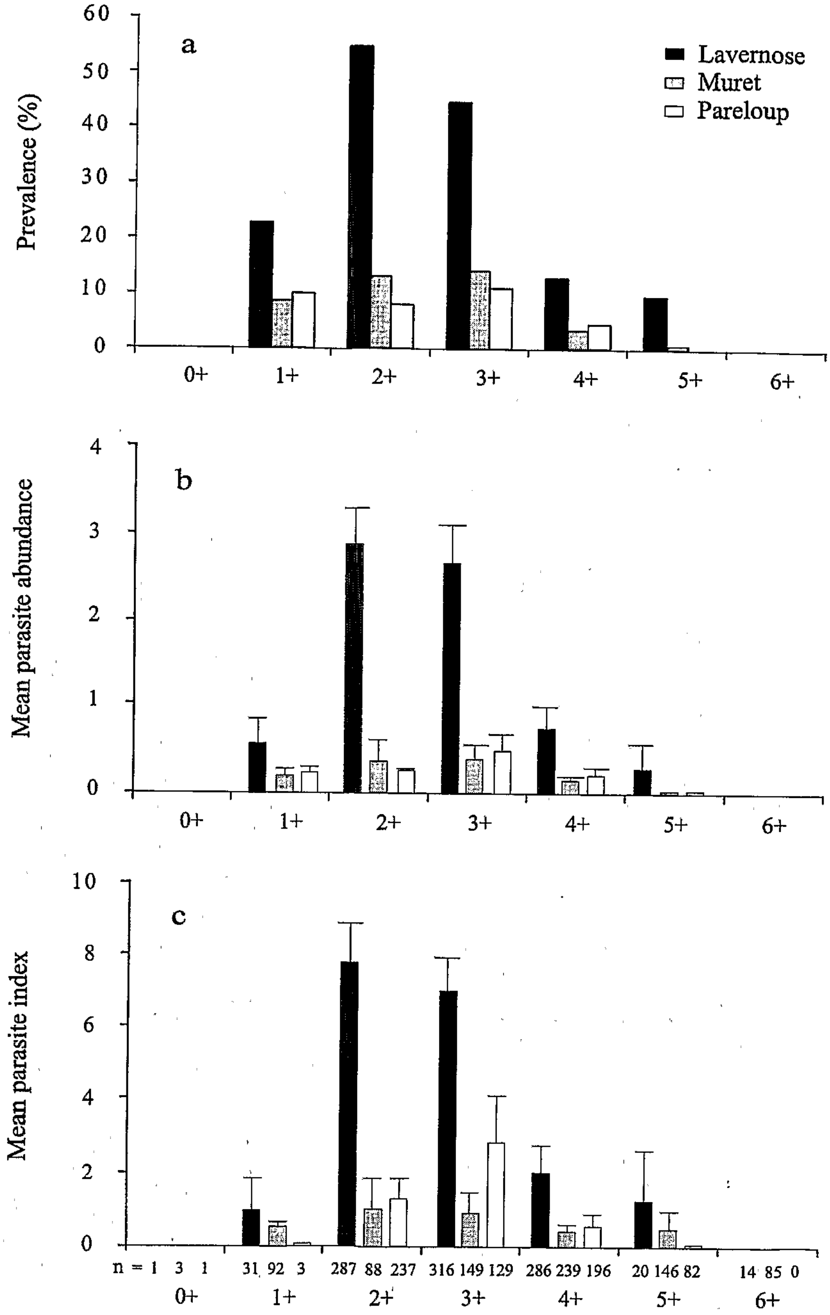

Fig.3. Change in a) prevalence b) mean parasite abundance and c) parasite load (I.P) for *Ligula intestinalis* plerocercoid larvae in relation with age of the roach, *Rutilus rutilus*, in the three localities surveyed : Lavernose and Muret gravel-pits and Pareloup lake. The vertical line on each histogram represents the 95 % confidence interval of the mean, and the number (n) of examined hosts is indicated.

Fig.3. Variation a) de la prévalence b) de l'abondance parasitaire moyenne et c) de la charge parasitaire (I.P) de la ligule, *Ligula intestinalis*, en fonction de l'âge du gardon, *Rutilus rutilus*, dans les trois localités étudiées : les gravières de Lavernose et de Muret et le lac de Pareloup. Les lignes verticales sur chaque histogramme représentent l'intervalle de confiance de la moyenne à 95 %, le nombre (n) d'individus hôtes examinés est indiqué sous le graphique.

tible to piscivorous birds predation than larger fishes with heavy loads, which are often too large to be captured. However, field studies have mentioned that fish harbouring plerocercoids of *L. intestinalis* experience an increased risk of being preyed upon by avian predators such as yellow herring gulls, *Larus cachinnans* (Harris & Wheeler 1974) and cormorants, *Phalacrocorax carbo* (Van Dobben 1952). These findings support the hypothesis that plerocercoids may alter the behaviour of fish in a way that favours its transmission to bird definitive hosts. For instance, infected roach may experience a higher risk of predation because of impaired motor performance, increased or decreased activity levels (Loot et al., in press, b) or by directly moving toward the microhabitats of foraging predators (Bean & Winfield 1992, Loot et al., in press, a).

Thus, parasites might reach the cost-benefit balance between heavy loads and single infections.

Lafferty (1999) suggested that parasites increasing trophic transmission in such complex life-cycles correspond to an adaptative strategy and questioned how it might evolve under different conditions.

To conclude, a better parasite transmission through food webs is probably a by-product of a subtle combination between the pathology exerted on the fish hosts, the modification of host (neuro)biology through hormonal control by parasites and host immune responses.

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