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Experimental evidence of asymmetrical competition between two species of parasitic copepods

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Lepeophtheirus thompsoni and *Lepeophtheirus europaensis* are two parasitic copepods naturally isolated on their sympatric hosts, i.e. turbot (*Psetta maxima* L.) and brill (*Scophthalmus rhombus* L.), respectively. They are able to meet, mate and hybridize on turbot experimentally, but they are naturally prevented from doing so by a strong host preference when given a choice. Theory suggests that such a pattern is possible, but only under conditions of competition for the resource. In the present study, the attachment rates of the two copepods were studied experimentally under various conditions of competition, infectious dose and number of available hosts. The results suggest a greater sensitivity to competition for the generalist species *L. europaensis* than for the specialist *L. thompsoni*, which is in agreement with theoretical predictions.

Keywords: ecology; competition; diversity; specialization; parasites; copepods

1. INTRODUCTION

Host–parasite systems offer useful models in the study of evolutionary ecology as the host represents the habitat–resource system of the parasite (Renaud 1992). In particular, host–parasite systems facilitate the study of diversity maintenance, ecological specialization and speciation mechanisms (Renaud *et al.* 1996; De Meeûs *et al.* 1998).

Two congeneric species of caligid copepod, *Lepeophtheirus thompsoni* (Baird, 1850) and *Lepeophtheirus europaensis* (Zeddam, Berrebi, Renaud, Raibaut and Gabrion, 1988), are parasitic on flatfish in the Gulf of Lions, western Mediterranean, France. *L. thompsoni* is naturally and experimentally specific for the turbot (*Psetta maxima* L., a marine scophthalmid) and *L. europaensis* infects both brill (*Scophthalmus rhombus* L., another marine scophthalmid) and flounder (*Platichthys flesus* L., a lagoono-estuarine pleuronectid). Flounder inhabits the brackish waters of lagoons and only enters the sea in winter for reproduction (De Meeûs *et al.* 1995). *L. europaensis* has never been found to infect turbot in the wild (Zeddam *et al.* 1988). However, both parasites can produce viable and fertile hybrids on turbot under experimental conditions (De Meeûs *et al.* 1990).

L. europaensis is a generalist parasite that displays broader ecological requirements, e.g. host range and salinity, than *L. thompsoni* (De Meeûs *et al.* 1993*a*). The fact that *L. europaensis* does not naturally infect turbot is partly explained by a strong host preference for brill when the choice between brill and turbot is available (De Meeûs *et al.* 1995). The observed diversity would be difficult to conceive without habitat (host) competition for the resource (host) (e.g. De Meeûs *et al.* 1993*b*). However, the existence of this competition still needs to be proven.

Hard selection (outside habitat regulation, i.e. no competition for the resource) favours habitat specialization and soft selection (within habitat regulation, i.e. competition for the resource) favours the evolution of generalists (Futuyma & Moreno 1988; De Meeûs *et al.* 1993*b*; Rausher 1993; De Meeûs & Renaud 1996). Thus, we expect *L. thompsoni* to be less sensitive to competition than *L. europaensis*. The objective of this study was to examine the existence and importance of competition for *L. thompsoni* and *L. europaensis* on turbot, their potentially shareable host. We undertook a series of experiments in order to test the settlement success of each species for different experimental conditions (i.e. infection dose, number of available hosts and time of introduction of each parasite species).

2. MATERIAL AND METHODS

(a) *Experimental hosts*

Parasite-free turbot (10 cm in length) were obtained from a fish farm in Brittany, France. The fish were anaesthetized with 3-aminobenzoic acid ethyl ester (Sigma A 5040, Sigma-Aldrich Chimie S.à.r.l, Saint Quentin, France) and examined microscopically in order to confirm their parasite-free status. Fish were stored in 50-l tanks.

(b) *Copepod collection and experimental infections*

The protocol for parasite collection and host infection was taken from De Meeûs *et al.* (1990). Ovigerous females were collected from infected fishes at the fishing port in Sète, France. *L. thompsoni* females were collected from the gill filaments of turbot and *L. europaensis* females were taken from the inner surface of the operculum and the wall of the gill chamber of brill. Egg clutches were transferred to individual Petri dishes (10 cm diameter) and incubated at 16 °C until the appearance of the copepodid (infectious) stage (see Boxshall (1974*a*) for a description of the life cycle).

Infective copepodids were counted and placed in 50-l tanks containing fishes under conditions of high aeration and no water flow. All fishes were anaesthetized, examined under the binocular microscope three days post-infection and the attached copepodids were counted.

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Table 1. *Description of and results obtained during the different experimental infections*

(n is the number of replicates and other abbreviations are as in §§ 2(d) and 3. For experiments marked with an asterisk, n_{Lt} and n_{Le} are presented in the same order.)

experiment type	n_T	i_{Lt}	i_{Le}	n	n_{Lt}	mean Lt	s.d. Lt	n_{Le}	mean Le	s.d. Le
Lt_A	1	50	—	12	19, 26, 33, 36, 41, 32	30.1	10.3	—	—	—
	—	—	—	—	44, 13, 26, 42, 16, 33	—	—	—	—	—
	1	100	—	6	79, 69, 105, 81, 76, 66	79.3	13.8	—	—	—
	2	50	—	12	32, 28, 24, 31, 41, 32	35.1	12.2	—	—	—
	—	—	—	—	40, 22, 51, 63, 35, 22	—	—	—	—	—
	2	100	—	6	83, 72, 96, 115, 72, 82	86.7	16.5	—	—	—
Le_A	1	—	50	12	—	—	—	12, 18, 20, 16, 24, 9	8.7	6.0
	—	—	—	—	—	—	—	17, 30, 18, 17, 29, 14	—	—
	1	—	100	6	—	—	—	32, 42, 21, 30, 19, 39	30.5	9.3
	2	—	50	12	—	—	—	19, 16, 17, 18, 28, 11	20.8	8.8
	—	—	—	—	—	—	—	16, 32, 40, 21, 20, 11	—	—
	2	—	100	6	—	—	—	40, 24, 41, 50, 34, 38	37.8	8.6
$LtLe^*$	1	50	50	12	23, 18, 44, 29, 31, 10	25.2	10.4	12, 6, 8, 8, 14, 12	7.1	4.2
	—	—	—	—	22, 40, 21, 14, 17, 33	—	—	7, 4, 3, 8, 0, 3	—	—
	2	50	50	12	29, 18, 23, 33, 35, 37	29.4	10.4	14, 9, 11, 7, 12, 12	9.6	3.6
	—	—	—	—	19, 50, 24, 42, 16, 27	—	—	2, 8, 12, 10, 5, 13	—	—
	2	50	100	6	30, 19, 54, 9, 20, 30	27.0	15.4	35, 6, 13, 50, 24, 34	27.0	16.0
Lt_D^*	2	50	50	12	32, 19, 20, 30, 23, 15	28.3	13.2	36, 22, 23, 20, 27, 28	23.75	8.6
	—	—	—	—	44, 60, 22, 17, 36, 21	—	—	22, 14, 29, 15, 10, 39	—	—
Le_D^*	2	50	50	12	53, 45, 55, 50, 35, 46	39.3	12.1	14, 2, 3, 12, 5, 12	8.7	5.0
	—	—	—	—	22, 43, 37, 16, 29, 41	—	—	14, 8, 10, 3, 16, 5	—	—

(c) *Neutral red staining of parasites*

In order to distinguish the two copepodid species when attached to the host, the larvae of *L. thompsoni* were stained with neutral red following the protocol of Anstensrud (1989, 1990), who showed that this treatment has no distinguishable effect on copepod behaviour.

(d) *Experimental protocols*

For single-species infections (Lt_A and Le_A in table 1), 50 or 100 *L. thompsoni* (Lt_A) or *L. europaensis* (Le_A) copepodids were administered to one or two turbot (see table 1 for details).

For infections with both parasite species simultaneously ($LtLe$ in table 1), turbot were simultaneously infected with *L. thompsoni* and *L. europaensis* (see table 1 for details).

For experiments with a delay in introducing one parasite species (Lt_D and Le_D), *L. europaensis* was first introduced and then *L. thompsoni* after 24 h (Lt_D), or *L. thompsoni* was first introduced and then *L. europaensis* after 24 h (Le_D) (see table 1 for details).

(e) *Statistical analysis*

The infestation success (i.e. the proportion of infectious larvae settled on the experimental host(s)) was analysed using generalized linear models (GLMs) with S-PLUS 2000 Professional Release 2$^{©}$ (MathSoft, Inc.). Stepwise procedures were used to retain the best models as described in *S-PLUS 2000 guide to statistics* (MathSoft, Inc. 1999). The stepwise process was undertaken in both directions (dropping–adding and adding–dropping). When the final models produced by these two procedures differed, we retained the most complete one. 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 (AIC) (from the lowest to the highest). As the response data corresponded to proportions, a classical binomial model was first fitted (e.g.

McCullagh & Nelder 1989). However, as residuals tended to be overdispersed (dispersion parameter ϕ greater than unity), a quasi-likelihood estimation was then used with a logit link function (i.e. $\log(\mu/(1-\mu))$) and a $\mu(1-\mu)$ variance function as suggested by *S-PLUS 2000 guide to statistics* (MathSoft, Inc. 1999; see also McCullagh & Nelder 1989; Hastie & Pregibon 1993). The significance of the different variables was thus tested by F-tests (e.g. Mathsoft, Inc. 1999).

Multiple comparisons were made with the 'simulation-based' method which was always the best of all the available ones in S-PLUS. The simulation-based method generates a near-exact critical point via Monte Carlo simulation and is substantially more efficient than other methods for non-standard families of comparisons or unbalanced designs (MathSoft, Inc. 1999).

3. RESULTS

For convenience, we have used the following abbreviations for the different variables and factors: n_T is the number of turbot in the experiment, Lt and Le are *L. thompsoni* and *L. europaensis*, respectively and expLt and expLe are the factors indicating to which kind of experiment Lt or Le were submitted, respectively. These factors are as follows.

(i) Lx_A, $LtLe$, Le_D and Lt_D: experiments with x (*L. thompsoni* or *L. europaensis*) alone, with both parasites simultaneously, with both parasites but *L. europaensis* delayed and with both parasites but *L. thompsoni* delayed.

(ii) i_{Lt}, n_{Lt} and %Lt: infection dose, number of attached copepodids and ratio of attached copepodids to infection dose, respectively, for *L. thompsoni*.

(iii) i_{Le}, n_{Le} and %Le: infection dose, number of attached copepodids and ratio of attached copepodids to infection dose, respectively, for *L. europaensis*.
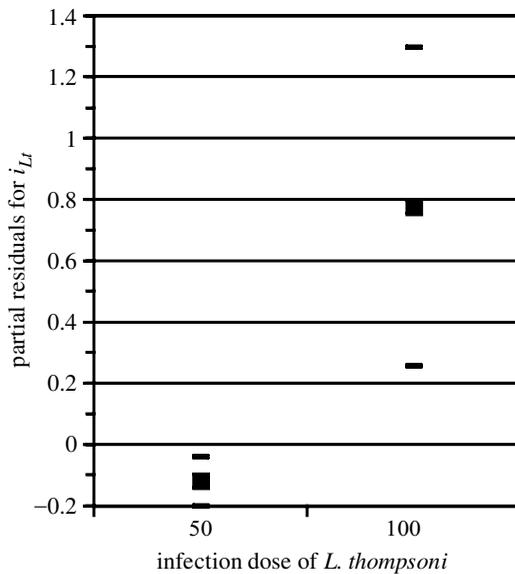
Figure 1. Influence of the infection dose (i_{Lt}) (50 or 100) on the attachment rates of *L. thompsoni* (as represented by their partial residuals extracted from the GLM regression). This variable represents 14.1% of the null deviance of the model. Partial fits and 95% confidence intervals are represented. Abbreviations as in the text.

The raw data are presented in the table 1.
For *L. thompsoni* the initial model was

$$\%Lt = i_{Lt} + \exp Lt + n_{Le} + n_{T} + i_{Le}$$
$$+ \text{(first-order interactions)} + \text{constant.} \quad (1)$$

Due to collinearity problems involving n_{Le} we could not stabilize the stepwise backward regression while changing variables' rank of entry in the model. n_{Le} was then regressed against all other variables and the residuals (Rn_{Le}) retrieved. These residuals where then introduced into the model in the place of n_{Le}.

Both backward and forward stepwise procedures converged to the same minimal model, i.e.

$$\%Lt = i_{Lt} + \exp Lt + \text{Cte}, \quad (2)$$

where Cte is a constant ($\phi = 9.95$, $r^2 = 0.23$ and null deviance $= 1305$ with d.f. $= 89$) ($F = 18$ and $p < 0.0005$ with d.f. $= 1$ for i_{Lt}, and $F = 4$ and $p = 0.012$ with d.f. $= 3$ for $\exp Lt$). Figure 1 shows an increase in *L. thompsoni* attachment rates with its infection dose. Figure 2 shows the effect of the experiment type. The multiple comparisons were significant only when simultaneous infections were compared to infections with *L. thompsoni* delayed (figure 2).

For *L. europaensis* the initial model was

$$\%Le = \exp Le + n_{T} + n_{Lt} + i_{Le}$$
$$+ \text{(all first-order interactions)} + \text{constant.} \quad (3)$$

Due to collinearity problems we had to work with the residuals (Rn_{Lt} and Ri_{Le}) from the two regressions of n_{Lt} and i_{Le} against the other variables.

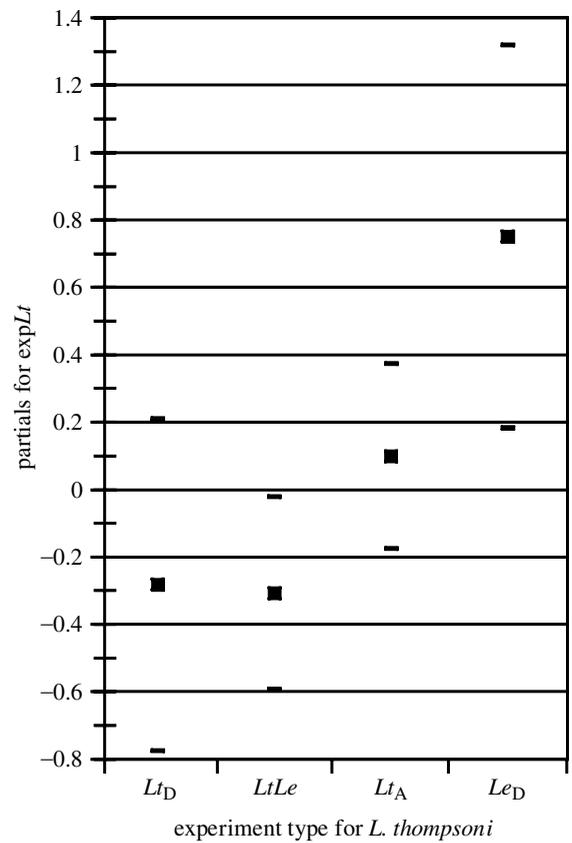After the dropping–adding (backward) procedure, the minimal model obtained was

Figure 2. Influence of the type of experiment ($\exp Lt$) for *L. thompsoni*'s attachment rates (as represented by their partial residuals). This factor represents 8.8% of the null deviance of the model. Partial fits and 95% confidence intervals are represented. Abbreviations as in the text.

$$\%Le = \exp Le + n_{T} + Rn_{Lt} + \text{Cte} \quad (4)$$
$$(\phi = 4.39 \text{ and AIC} = 444).$$

After the adding–dropping (forward) procedure the minimal model obtained was

$$\%Le = \exp Le + n_{T} + \text{Cte} \quad (5)$$
$$(\phi = 4.57 \text{ and AIC} = 449).$$

Thus, the model retained was

$$\%Le = \exp Le + n_{T} + Rn_{Lt} + \text{Cte.} \quad (6)$$

($r^2 = 0.44$, $F = 21$ and null deviance $= 702$ with d.f. $= 89$) ($F = 21$ and $p < 0.0005$ with d.f. $= 3$ for $\exp Le$, $F = 6$ and $p = 0.02$ with d.f. $= 1$ for n_{T}, and $F = 3$ and $p = 0.08$ with d.f. $= 1$ for Rn_{Lt}).

The weak, negative effect of n_{Lt} can be seen in figure 3 and, despite its lack of significance, it appears to play an important role in the model when other variables are present. The number of available hosts (n_{T}) has a significant but weak positive effect on *L. europaensis* attachment rates (figure 4). The experiment type (figure 5) has a predominant effect (38.8% of the deviance) and is highly significant. The significant multiple comparisons between experiment types isolate two groups: (i) [Lt_{D} and $LtLe$] (strong competition for *L. europaensis*) and (ii) [Le_{A} and Lt_{D}] (no or weak competition for *L. europaensis*). These results suggest strong competitive effects.
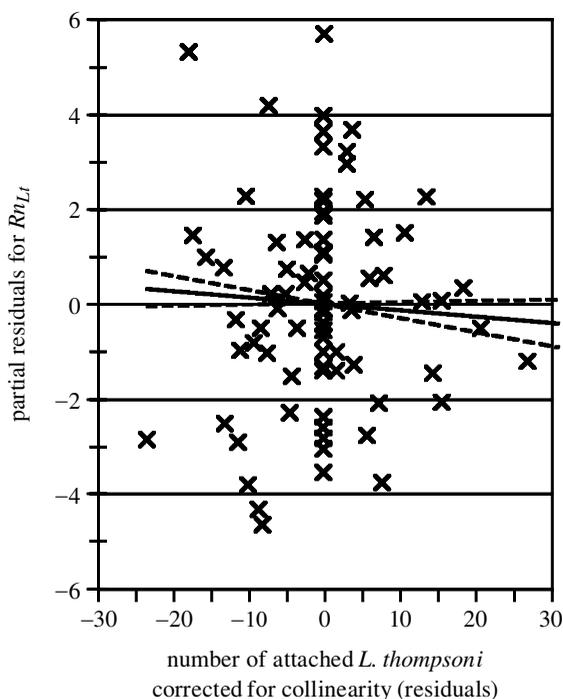
Figure 3. Influence of the number of attached *L. thompsoni* (n_{Lt}) corrected for collinearity (residuals Rn_{Lt} of the regression $n_{Lt} = \exp Le + n_T + i_{Le}$) on the attachment rates of *L. europaensis* (as represented by their partial residuals). This factor represents less than 2% of the null deviance of the model. Partial residuals, partial fit and 95% confidence intervals are represented. Abbreviations as in the text.
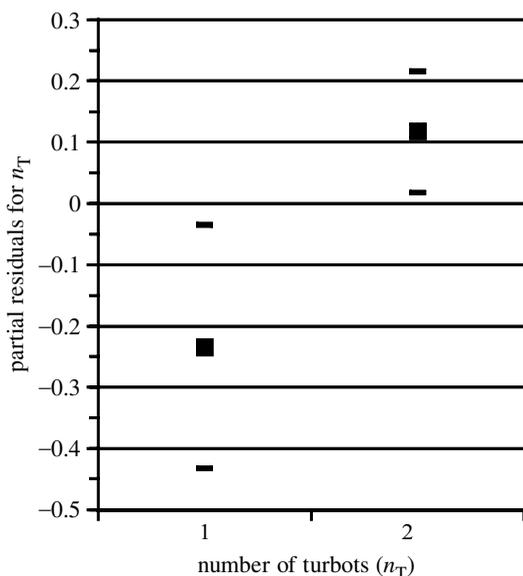

Figure 4. Influence of the number of hosts (n_T) (one or two) on the attachment rates of *L. europaensis* (as represented by their partial residuals). This factor represents 3.5% of the null deviance of the model. Partial fits and 95% confidence intervals are represented. Abbreviations as in the text.

Finally, it can be noted from figure 6 that, as previously demonstrated (De Meeûs *et al.* 1990, 1993a), *L. europaensis* can easily infect an alternative host (turbot), but with a lower success than *L. thompsoni*.
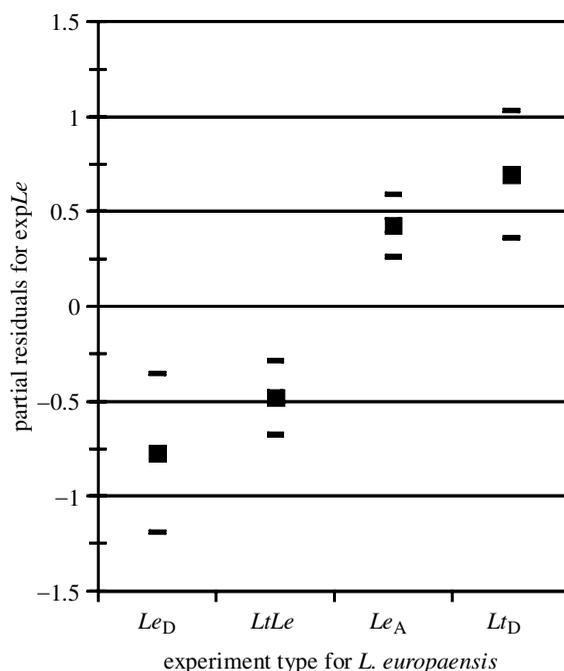
Figure 5. Influence of the experiment type ($\exp Le$) on *L. europaensis* attachment rates (as represented by their partial residuals). This factor represents 38.8% of the null deviance of the model. Partial fits and 95% confidence intervals are represented. Abbreviations as in the text.

4. DISCUSSION

The two flatfish turbot and brill are parasitized in the Atlantic Ocean by the same sea lice as in the Mediterranean Sea (Zeddam *et al.* 1988), but flounder is exploited by two other copepod species, *Lepeophtheirus pectoralis* and *Acanthochondria depressa* (Boxshall 1974b), which are absent from the Mediterranean flounder. All three hosts are of northern origin (Quignard 1972). They colonized the Mediterranean Sea during the course of the last glaciation events, during which flounder may have lost their original parasites and become infected with *L. europaensis* from brill (De Meeûs *et al.* 1990). The absence of *L. europaensis* on flounder in the Atlantic suggests that parasite competition has a role in determining the host range for these copepods (De Meeûs *et al.* 1995), but there is no direct evidence for the effect of such competition.

During these experiments, the major factor found to influence *L. thompsoni* host colonization positively was the infection dose. This effect is consistent with aggregative behaviour of the infective stages, which might reflect a mating advantage. Previous work has shown that such a mechanism has the potential for generating aggregative distribution of parasites such as sea lice (e.g. Boxshall 1974c). Selection for enhancing intraspecific contact in parasites (e.g. Rohde 1979) and even in free-living copepods (Heip & Engels 1977) is known. The fact that the fixation rate of *L. thompsoni* on its host is affected by the experiment type (mainly when *L. europaensis* is delayed) is probably the sign of an influence of interspecific competition, although the signal is weak. The total deviance in *L. thompsoni* fixation rates remains poorly
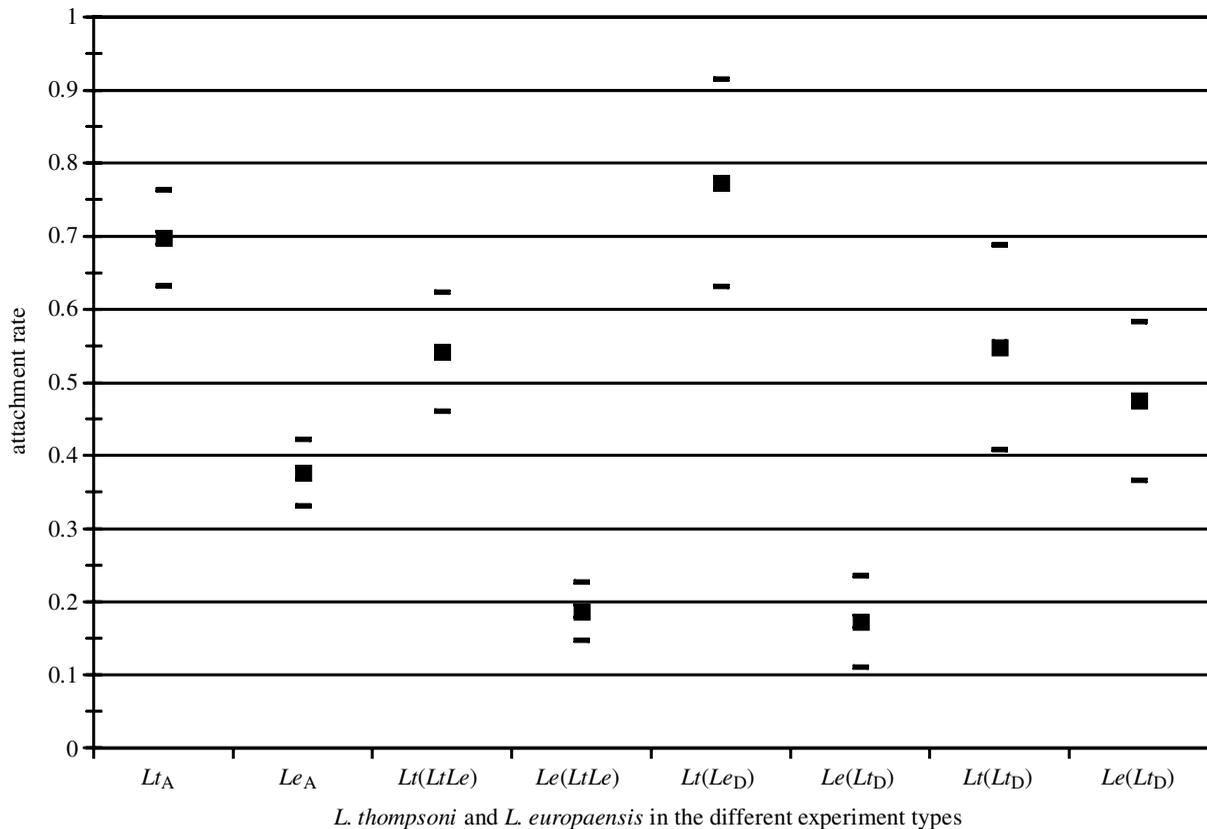
Figure 6. Means and 95% confidence intervals for the attachment rates of the two copepod species in the different experiment types (data uncorrected for other effects). Abbreviations as in the text.

explained and it seems that between-replicates variation (individual host variability?) could be responsible for most of the variation.

The major factor influencing *L. europaensis* attachment rates is the experiment type, in particular if *L. thompsoni* is absent or delayed (strong positive effects). Interestingly, only in the latter case (*L. thompsoni* delayed) does *L. europaensis* attain attachment rates that are comparable to those of *L. thompsoni*. Moreover, the part of the deviance explained for *L. europaensis* is nearly twice of that of *L. thompsoni*. This is in agreement with a much stronger impact of interspecific competition on the attachment rate of *L. europaensis*. The positive effect of an increase in available hosts on *L. europaensis* attachment confirms the existence of such competition at an intraspecific level.

Host immunity has been suggested in the case of favourable survival of another copepod, *Lepeophtheirus salmonis*, on sea trout (*Salmo trutta* L.) compared with survival of the same parasite on Atlantic salmon (*Salmo salar* L.) (Dawson *et al.* 1997). However, in the present work the number of settled *L. thompsoni* copepodids weakly influences *L. europaensis* settlement and, moreover, the infectious dose of *L. thompsoni* displays a positive influence on itself. These observations do not support a preponderant role for immunity in the competitive influence of *L. thompsoni* over *L. europaensis*.

Hull *et al.* (1998) showed that ablation of the antennule tip of *L. salmonis* resulted in loss of response of the copepods to host odours and profoundly affected resettlement on the host, pair formation and mating. Such

phenomena may account for the detection and attraction of individuals of the same species by *L. thompsoni* copepodids and the repulsive effect of *L. thompsoni* on *L. europaensis* copepodids. It may also explain the stimulating effect that a delayed introduction of *L. europaensis* seems to have on the *L. thompsoni* fixation rate.

Furthermore, De Meeûs *et al.* (1993*a*, 1995) demonstrated that *L. thompsoni* (which is intolerant to brill and flounder) and *L. europaensis* (which is tolerant to brill, flounder and turbot) are maintained on their sympatric hosts by the existence of a strong habitat selection of Doyle's (1975) type. However, the required regulation by density dependence in each habitat (within-host competition) remains to be proven. Our results confirm the role of density dependence in species with different sensitivity to competition (Rosenzweig's (1991) asymmetrical competition). The ability of the tolerant *L. europaensis* in colonizing turbot when it is alone strongly decreases when the intolerant competing species, which is only able to exploit turbot, is added.

In conclusion, the present biological model is in accordance with a model of density-dependent habitat selection of competing species and, in particular, with asymmetrical competition between specialist and generalist species, where the generalist is expected to be more sensitive to competition than the specialist (Futuyma & Moreno 1988; De Meeûs *et al.* 1993*b*; Rausher 1993; De Meeûs & Renaud 1996). Our results confirm the role of interspecific competition in the maintenance of *L. thompsoni* and *L. europaensis* on their respective natural hosts, preventing turbot invasion by *L. europaensis*.

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