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The Distribution and Abundance of *Lernaeocera lусi* (Copepoda) on Hake (*Merluccius merluccius*) and Bib (*Trisopterus lусus*) (Teleostei)

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Abstract—Tirard C., Thomas F., Raibaut A. & Renaud F. 1996. The distribution and abundance of *Lernaeocera lусi* (Copepoda) on hake (*Merluccius merluccius*) and bib (*Trisopterus lусus*) (Teleostei). *International Journal for Parasitology* 26: 1387–1392. Distribution patterns, mean intensity and prevalence of *Lernaeocera lусi* (Copepoda, Pennellidae) in its 2 hosts *Trisopterus lусus* (Teleostei, Gadidae) and *Merluccius merluccius* (Teleostei, Merlucciidae) were examined, together with parasitic abundance and aggregation in relation to the size of the host. The mean parasite abundance and the variance to mean abundance ratio increased with host size, suggesting that the accumulation of this parasite had no noticeable impact on the structure of either host population. *Merluccius merluccius* being a newly colonized host in the Mediterranean, these results are discussed in relation to current ideas on the evolution of pathogenicity in heterospecific associations. Copyright © 1996 Australian Society for Parasitology. Published by Elsevier Science Ltd.

Key words: Copepoda; *Lernaeocera*; Teleostei; *Trisopterus*; *Merluccius*; survival; ecology; evolution.

INTRODUCTION

Parasitism is recognized as a factor that influences animal communities (Anderson & Gordon, 1982; Scott & Dobson, 1989; Minchella & Scott, 1991). Parasites can act directly on host survival and demography or have indirect effects on host physiology and behaviour that interfere with competition and predation (Freeland, 1983; Scott, 1987; Price, Westoby & Rice, 1988; Washburn, Mercier & Anderson, 1991; Jaenike, Benway & Stevens, 1995; Thomas *et al.*, 1995).

A common hypothesis in parasitology is that the pathological and demographical impact associated with a host–parasite pair diminishes with time. Until recently, there was such a general agreement with the assumption that “successful” parasite species evolve

to be harmless to their hosts, that it worked as a paradigm. Some harmful interactions were indeed demonstrated to be new, or at least more recent than comparable benign interactions (see Toft & Karter, 1990 for review).

However, this dogma was criticized by several people who explored theoretical aspects of the population genetics and population dynamics of host–parasite associations and conceived different modes of evolution (Anderson & May, 1982; Toft & Karter, 1990; Renaud & De Meeus, 1991; Combes, 1995). In fact, few biological models offer valuable evidence or objective insight into how pathogenicity evolves, mainly because testing a hypothesis requires a model allowing the comparison of 2 different aspects of host population responses, past and present.

A previous study (Tirard *et al.*, 1993) revealed the existence of an old host–parasite pair in the Atlantic, *Trisopterus lусus* (L., 1758) (Teleost. Gadidae)–*Lernaeocera lусi* (Bassett-Smith, 1896) (Copepod, Pennellidae), and of a newer host–parasite pair involving

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the same parasitic species in the Mediterranean. Indeed, we showed that this parasitic copepod colonized a new host, *Merluccius merluccius* (L., 1758) (Teleost, Merlucciidae) in the Mediterranean (Tirard *et al.*, 1993). The transfer to this new host must have been a recent event, since *L. luscus* was introduced to the Mediterranean during the last glaciations with its host *T. luscus*, an ice-age immigrant of northern origin which moved south from its habitat (Quignard, 1972; Tirard *et al.*, 1992, 1993).

Copepods of the genus *Lernaecocera* have a 2-host life cycle (Kabata, 1979): mating occurs on a Pleuronectiform fish and the fertilized female leaves the initial host to colonize a Gadiform fish. Once attached to the second host, the highly modified adult female becomes haematophagous, which might cause host mortality (Kabata, 1970, 1984; Sundness, 1970; Van den Broek, 1978; Khan, 1988; Khan & Lee, 1989; Khan, Lee & Barker, 1990; Khan *et al.*, 1993). Generally, mortality induced by parasitic copepods was shown to be a function of parasite burden (Kabata, 1981).

The aim of the present study, based on data collected in the field, is to evaluate the influence of *L. luscus* on survival of its 2 hosts. The hypothesis that host-parasite "coevolution" reduces the pathogenic effect of parasites on their hosts allows expectation of a weaker impact on the ancestral host, *T. luscus*, than on the newer one, *M. merluccius*.

MATERIALS AND METHODS

Geographical location. Large samples of hake, *M. merluccius* ($n=792$) and bib, *T. luscus* ($n=285$), were collected by bottom-trawling on the continental shelf in the Gulf of Lions (Mediterranean) and in the Bay of Biscay (Atlantic), respectively.

Occurrence and abundance of parasites. In the laboratory, total fish length (L_t) was measured to the nearest mm, and gills were examined for parasites. The usual attachment site of *L. luscus* on gadiform fish is the gill arch (Kabata, 1979).

All parasitic individuals, including the infective Pennella stages described by Sproston (1941), were recorded for calculation of overall indices of parasitism, prevalence (p) and mean intensity (I) (Margolis *et al.*, 1982).

All statistical tests used in the present study are described in Sokal & Rohlf (1981). All tests were 2-tailed and results were considered to be significant at the 5% level.

Analysis of the influence of parasitism on host survival. The impact of the Pennella stages on the host was assumed to be negligible. Thus, only the haematophagous females were included in the analysis of the influence of *L. luscus* on host survival. The model described by Anderson & Gordon (1982) and Rousset *et al.* (in press) enables the inference of mortality in free-ranging populations, by examining changes in mean parasite abundance (Margolis *et al.*, 1982) and variance to mean abundance ratio (β), as a function of host age. Since there is a good relation between age and size for both fish species [Bruno *et al.*, 1979; Puente, 1988; Merayo & Villegas, 1994; Oliver P. 1991. Dinámica de la población de la merluza

(*Merluccius merluccius* L.) de Mallorca (reclutamiento, crecimiento y mortalidad). Doctoral thesis, Universidad de las Islas Baleares, Mallorca, Spain], host size classes were used to study the relation between parasitism and host age.

- Individuals belonging to the species *T. luscus* were placed in 7 length classes. We selected a step between classes equal to 3.3 cm. Classes 1 and 7 included all individuals smaller than 14 cm or larger than 30.8 cm, respectively.
- Individuals belonging to the species *M. merluccius* were placed in 11 length classes. These classes consisted of steps of 2.1 cm. All individuals smaller than 9.6 cm and all individuals larger than 29 cm were grouped into class 1 and class 11, respectively.

For both fish species, mean parasite abundance and variance to mean abundance ratio (β) were calculated separately for each host size class. To determine the relation between those parameters and host age, we fitted linear and non-linear (logarithmic, polynomial and exponential) regressions to the set of points and retained the regression which explained the highest amount of variation.

RESULTS

Distribution, prevalence and intensity of L. luscus

L. luscus displayed an aggregated dispersal pattern in its 2 hosts (Fig. 1).

The observed frequency distributions of the parasite on *T. luscus* and on *M. merluccius* conformed to a negative binomial distribution (Kolmogorov-Smirnov test: $D=0.02$ and $D=0.01$, respectively, $P>0.05$ in both cases).

The aggregation coefficient (k) was 0.34 for *T. luscus* and 0.25 for *M. merluccius*.

The prevalence of parasitism (p) was 32.3% in the *T. luscus* sample ($n=285$), and 29.7% in the *M. merluccius* sample ($n=792$): these 2 values are not significantly different (Fisher's exact test, $P=0.57$).

The mean intensity (I) was 2.31 ± 2.22 ($n=92$) and 2.87 ± 3.18 ($n=234$) on *T. luscus* and *M. merluccius*, respectively. No significant difference was found in the mean intensity between the 2 hosts (Mann-Whitney U-test, $U=9584.5$, $P=0.11$).

Changes in mean parasite abundance and β with host age

Trisopterus luscus. The abundance increased steadily with size and reached a maximum level of 1.67 (Fig. 2a). The variance to mean ratio (β) increased concomitantly with the abundance until attaining a value of 4.63 for the largest size class (>30.8 cm) (Fig. 2b).

Merluccius merluccius. The highest mean number (1.79) occurred in the next to the largest size class (Fig. 2c). The abundance calculated for the largest size class (>29 cm) was a lower value of 0.86, whereas

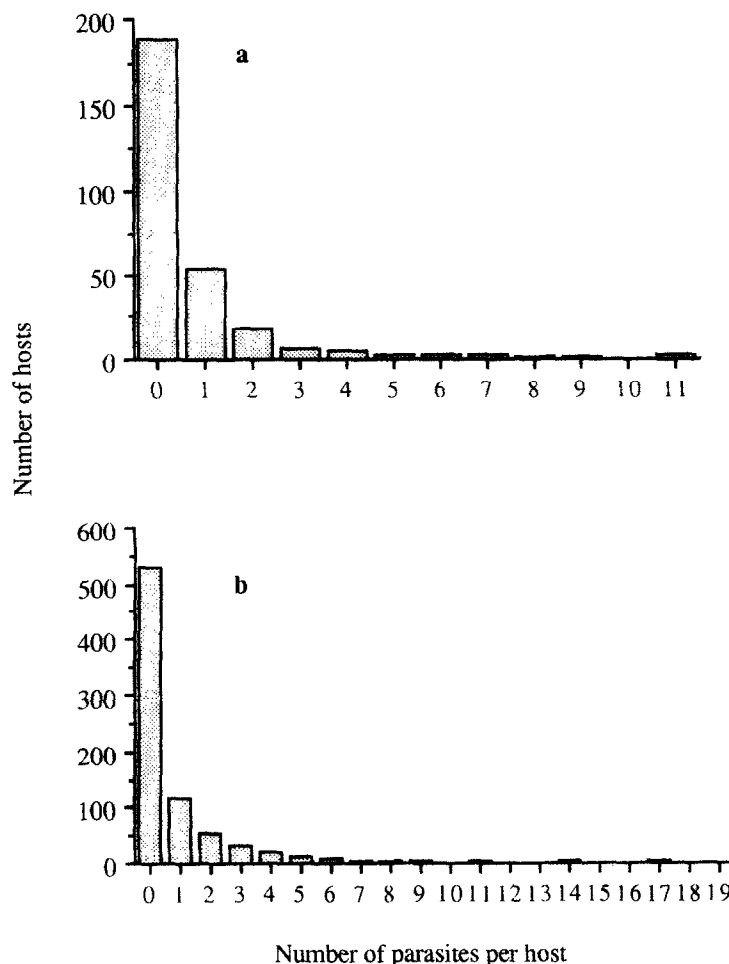


Fig. 1. Frequency distribution of *Lernaecera lusci* on (a) *Trisopterus luscus* and (b) *Merluccius merluccius*.

the variance to mean ratio reached its maximum level of 14.30 in that same class (> 29 cm) (Fig. 2d).

For both fish species and both parameters, fits were carried out better by means of non-linear regression than by simple linear regression (data not shown). A clear positive relationship was shown to exist between host size and mean abundance of *L. lusci* (Fig. 2a, c) and between host size and aggregation (β) (Fig. 2b, d). The fitted curves did not show any decrease with host age.

DISCUSSION

Lernaecera branchialis, which parasitizes Gadidae living in the Arctoboreal region, has often been associated with host mortality (Kabata, 1970, 1984; Sundness, 1970; Van den Broek, 1978; Khan & Lacey, 1986; Khan *et al.*, 1990) and host growth reduction (Khan, 1988; Khan & Lee, 1989; Khan *et al.*, 1993).

Based on predictions by Anderson & Gordon

(1982) and Rousset *et al.* (in press), *Lernaecera lusci* does not appear to exert a regulatory influence in *M. merluccius* or *T. luscus*. Indeed, when host mortality is positively correlated with parasite accumulation (Anderson & Gordon, 1982; Rousset *et al.*, in press) or simply with parasite presence (Rousset *et al.*, in press), a maximum level of abundance and dispersion occurs in hosts of intermediate age. Curves of the parasite abundance or aggregation as a function of host age are convex, as a consequence of the death of the oldest infected hosts. In the present study, an increase in mean abundance and aggregation with age was clearly evident for both fish species.

Parasitism by *L. lusci* does not seem to have an impact on fish growth either. A parasite-induced growth reduction would tend to increase the parasitic burden in smaller length classes (Rousset *et al.*, in press), which is not consistent with our observations.

Explanations for the observed increase of parasite abundance with host size are that older fish (i) have

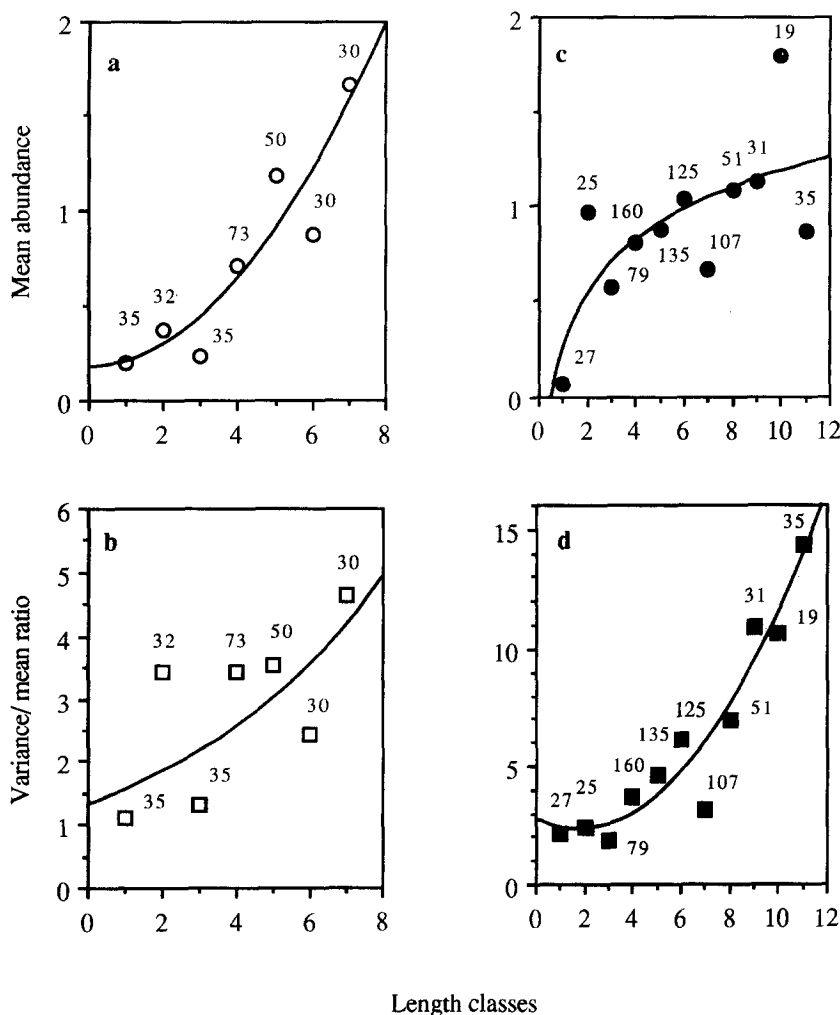


Fig. 2. Mean parasite abundance and variance to mean abundance ratio of *Lernaocera luscii* in relation to host size in *Trisopterus luscus* (a, b) and *Merluccius merluccius* (c, d). The number of hosts analysed in each length class is indicated above each point. The equations for regression curves are: a/ $y = 0.17 + 0.006X + 0.028X^2$ $r^2 = 0.85$ $n = 7$. b/ $y = 1.31 \times 10^{(0.07X)}$ $r^2 = 0.42$ $n = 7$. c/ $y = 0.92 \log X + 0.26$ $r^2 = 0.50$ $n = 11$. d/ $y = 2.75 - 0.49X + 0.13X^2$ $r^2 = 0.91$ $n = 11$.

been exposed to parasites for a longer period of time, which increased their chances of acquiring and accumulating parasites (e.g. Anderson & Gordon, 1982; Rousset *et al.*, in press) and (ii) provide space on the branchial arches adequate for parasite accumulation (Van den Broek, 1979; Etchegoin & Sardella, 1990; Poulin, Curtis & Rau, 1991). The most plausible explanation for the concomitant increase in parasite abundance and dispersion is that *M. merluccius* and *T. luscus* are continually acquiring the parasite through time. If there is a phenomenon such as mortality eliminating infected hosts, it must not be severe enough to consider *L. luscii* an important biotic constraint.

Merluccius merluccius, which is a more recent host for *L. luscii*, appears to be a favourable resource for this parasite, since similar indices of parasitism were

calculated on this new host in the Mediterranean and on the ancestral host, *T. luscus*, in the Atlantic.

Lernaocera luscii does not appear more injurious to the derived host in the Mediterranean than to the ancestral one in the Atlantic. Surprisingly, De Meeus *et al.* (1995), who studied a model providing similar evolutionary aspects of host-parasite relationships, demonstrated that the impact of the copepod *Lepophtheirus europaensis* was higher on its ancestral host, the brill *Scophthalmus rhombus*, than on the derived one, the flounder *Platichthys flesus*. These 2 studies on parasitism of marine fishes seem to contradict the common hypothesis of higher virulence associated with a recent association between a host and its parasite. Two recent works on the evolution of parasites or host-parasite relationships (Poulin, 1995;

Morand, Manning & Woolhouse, 1996) emphasized the necessity to question the generality of some old rules, which still remain widely accepted by parasitologists.

However, it is still possible that the parasite has a greater impact on the newer host, *M. merluccius*, but that this impact concerns a different aspect of host fitness. For instance, an impact on host reproduction would not be apparent from survivorship data and would not be detected by our analysis.

Another possible explanation for our results would be that the transfer to *M. merluccius* in the Mediterranean may not be recent on an evolutionary time scale. *Merluccius merluccius* is certainly a newer host, but we do not know the absolute time scale for evolutionary and co-evolutionary events. We have to consider the possibility that the inability to detect a heavier impact of the parasite on *M. merluccius* was due to the fact that host and parasite have had time to co-evolve, since there is evidence that co-evolution may occur quite rapidly in some cases (Boray, 1969; Schom, Novak & Evans, 1981).

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