Differential mortality of two closely related host species induced by one parasite

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SUMMARY

Understanding the importance of parasites in affecting the biodiversity of host species in ecosystems is a central aim of conservation biology. Recent advances in ecology have suggested that differential parasite susceptibilities between taxonomically related host species may be a determinant of animal community structure. Although conceptually appealing, such an hypothesis suffers from a lack of field evidence. Here, we report that the populations of two congeneric and sympatric host species (*Gammarus insensibilis* and *G. aequicauda*), infected by the same parasite (*Microphallus papillorobustus*), exhibit a strongly contrasted pattern of parasite-induced mortality.

1. INTRODUCTION

Recent advances in ecology have suggested that parasites are important determinants of community and population structure (Barbehenn 1969; Price 1980; Freeland 1983; Minchella & Scott 1991). For example, parasites that preferentially infect a competitively dominant host species, can lead to increased species diversity within ecosystems (Ayling 1981). When nutrients are scarce, parasitic infections can relax host competition by reducing host abundance (Washburn 1991). Paradoxically, few quantitative data are available on how these organisms affect host mortality in nature (Scott & Dobson 1989). Parasite-induced host mortality is particularly difficult to demonstrate in the field; moreover, parasites can affect host fitness in many ways (Price 1980). Pathology due to parasitic infection can directly reduce host survival (Goater & Ward 1992) or its reproductive potential (Kuris 1974; Baudouin 1975). Parasites may also kill their hosts by increasing their susceptibility to predation (Holmes & Bethel 1972) or by reducing their competitive fitness (Park 1948). In addition, some parasites are known to enhance their host sensitivity to pollution (Sakanari *et al.* 1984; Brown & Pascoe 1989).

Taxonomically related host species are generally likely to be susceptible to infection by the same parasites species (Park 1948; Blackmore & Owen 1968; Segun 1971; Awachie 1972; Freeland 1983). However, species of parasite do not usually infect hosts species at statistically similar frequencies (Freeland 1983) and/or virulence differs from one species to another (Park 1948; Anderson & Lankester 1974; Price 1980). Thus, in the field a host species whose fitness is impaired by parasitism is at a selective disadvantage in competition with a closely related but relatively unaffected species. Currently, convincing evidence of such phenomena on closely related host species comes from laboratory experiments (see, for example, Park 1948; Utida 1953). Although differential parasite susceptibility between sympatric and congeneric host species has already been demonstrated in the field (Coustau *et al.* 1991; Le Brun *et al.* 1992), no study clearly demonstrates a differential parasitic effect on the survival of congeneric host species.

Microphallus papillorobustus (Trematoda, Microphallidae) is a parasite known to infect two congeneric and sympatric host species, the amphipods *Gammarus insensibilis* and *Gammarus aequicauda* (Helluy 1983*a*). In the case of *G. insensibilis*, however, once infective larvae (cercariae) have entered the gammarids through the branchial cuticle they systematically migrate to the amphipod's brain, encyst in cerebroid ganglions and consequently strongly alter their host behaviour (Helluy 1983*a,b*). In infected gammarids, phototaxis becomes strongly positive and geotaxis is reversed from positive to negative. In addition, responses to mechanical disturbances are altered: gammarids skim along the water surface and/or cling to surface material. Experimentally, infected individuals are more vulnerable than uninfected ones to predation by gulls (Helluy 1984), the definitive hosts of *Microphallus papillorobustus*. In *G. aequicauda*, such 'suicidal' behaviour can be induced by the parasite only if parasitic infection occurs during the host's juvenile stage. Later, cercariae do not migrate to the brain, instead they encyst in the body where they do not provoke behavioural alterations (Helluy 1983*a*).

To analyse parasitic effects on host population, we investigated the existence of parasite-induced host mortality by examining the frequency distribution of the trematode *Microphallus papillorobustus* in its two possible intermediate hosts.

2. METHODS

Large samples of *G. insensibilis* ($n = 1115$) and *G. aequicauda* ($n = 929$) were collected during spring 1994 (Palavas les flots, Southern France, 43° 25′ N, 3° 35′ E). Gammarids were randomly sampled in the aquatic vegetation and in no more than 40 cm water depth. All individuals were immediately preserved in alcohol (70 %). Later they were identified, sexed, measured for length and dissected to count the number of *Microphallus papillorobustus* metacercariae present. As expected, the metacercariae in *G. insensibilis* were always found in the gammarid cerebrum whereas they were mainly found in the body in *G. aequicauda*. We estimated: (i) the mean parasite abundance (MPA) (Margolis *et al.* 1982) defined as the total number of parasites divided by the total number of hosts examined; and (ii) the variance to mean abundance ratio, β (a measure of aggregation, Margolis *et al.* 1982). Growth in gammarids conforms to a logistic curve (Sutcliffe *et al.* 1981) but the relation between size and age depends largely on temperature, food and sex (Sutcliffe *et al.* 1981). Here, the males and females of the two species were placed in eight length classes (assuming there was a close relation between age and size). In classes 2–7, steps are equal (i.e. *G. aequicauda*: male = 1 mm, female = 0.5 mm; *G. insensibilis*: male = 2 mm, female = 1.5 mm). Class 1 includes all those individuals that are too small to be in class 2, and class 8 includes all those individuals that are too large to be in class 7. We then analysed changes in mean parasite abundance and in β with host size.

3. RESULTS

Changes in MPA of *Microphallus papillorobustus* with host size are shown in the figure 1. In *G. aequicauda*, MPA increased steadily with host size in both males and females. The maximum number of metacercariae recorded was 53.2 and 43.1, for males and females respectively. Conversely, in *G. insensibilis*, MPA peaked in the medium-sized individuals and the maximum number of metacercariae recorded was 3.8 in males and 3.1 in females. The variance to mean abundance ratio, β, reflects the degree of parasitic aggregation within the host. In *G. aequicauda* and in each sex, this ratio value increased steadily with host size. In *G. insensibilis*, concomitant with the decline of MPA in the highest length classes, the degree of dispersion also tends to decrease in value for males as for females.

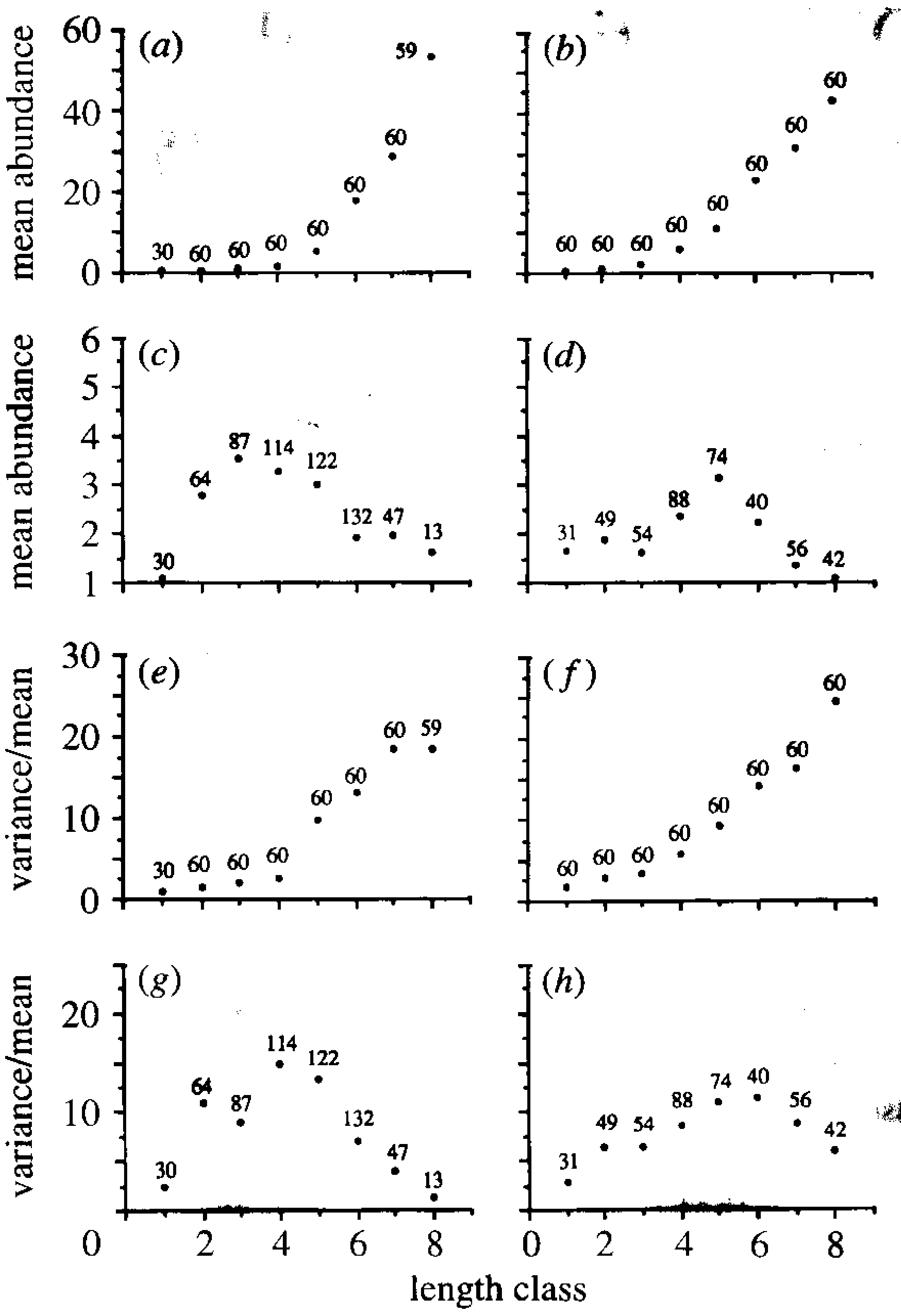

Figure 1. Mean parasite abundance and the variance to the mean abundance ratio (β) of *Microphallus papillorobustus* in relation to host size in *Gammarus aequicauda* (*a*,*b*,*e*,*f*) and *G. insensibilis* (*c*,*d*,*g*,*h*). The number of host analysed in each length classes are indicated above each dot. Left hand columns detail data for males, the right hand column females.

4. DISCUSSION

These data demonstrated, for the same parasite species, the existence of two distinct infection patterns through two congeneric and syntopic host species. In *G. aequicauda*, our results suggest that *M. papillorobustus* has no significant effect on survival compared to *G. insensibilis*. Indeed, when the host death rate is independent of parasite burden, the continued parasite acquisition through time acts to increase the parasite intensity in older classes (Anderson & Gordon 1982). Such a result corresponds to what is observed for *G. aequicauda*. However, when the rate of mortality is positively correlated with parasite burden, a maximum abundance occurs in hosts of intermediary age and fall in the older age classes (Anderson & Gordon 1982), as it is observed here for *G. insensibilis*. In addition, the value of the degree of dispersion also tends to decrease for *G. insensibilis*, suggesting that heavily infected individuals are severely removed from the population (Anderson & Gordon 1982; Gordon & Rau 1982).

Among the possible alternatives to the hypothesis of parasite-induced host mortality, age-related diminution in the average rate of infection in *G. insensibilis* fails to explain our results. A decline of mean parasite abundance would require mechanisms eliminating cercariae once encysted in the gammarid cerebrum. Parasite-induced growth reduction in *G. insensibilis* could explain the decreased abundance value, and the concomitant decline of β in larger length classes. However, the resulting impact on gammarid fitness would be the same as being killed. Indeed, female fecundity largely depends on the size (Ward 1988), and in male only larger individuals access to mates (Ward 1983, 1984, 1988). From the host's perspective, such an infection would be thus evolutionary equivalent to death.

Studies on parasites that enhance their host susceptibility to predation by definitive hosts ('favorization' according to Combes 1991) have not provided much quantitative field data so far. Consequently, the demographic impact of such a parasitism is still unknown. This distinct impact on host mortality between the two gammarid species coincides with a differential virulence of *M. papillorobustus*. Gammarids with altered behaviour have a higher susceptibility to predation by gulls (Helluy 1984) and perhaps fishes: large individuals are known to have a greater risk of predation (Sutcliffe 1993). The concomitant decline of mean parasite abundance and β in large classes may thus indicate that predators preferentially eat large infected gammarids. In addition, freshwater gammarids with altered behaviour consume less food and are more sensitive to toxicants (Brown & Pascoe 1989). Thus pathology associated with infection may directly affect the gammarid vigor and enhance the mortality rate, without the need to invoke predation. Furthermore, we can suspect for the previous reason that individuals with altered behaviour are at a selective disadvantage in intraspecific and/or interspecific competition compared to uninfected individuals.

Parasitism has received little attention in ecological studies of gammarid communities (Dick & Elwood 1992; Busdosh *et al.* 1982). By affecting survival in such a way, *M. papillorobustus* might act as an important mechanism regulating the density of *G. insensibilis* populations. Interestingly, *G. insensibilis* and *G. aequicauda* frequently coexist in the same habitat (Brun 1971; Janssen *et al.* 1979; Helluy 1981). The greater reproductive success of *G. insensibilis* (Janssen *et al.* 1979) is thus compensated by a higher tolerance to disease of *G. aequicauda*. In such a context, *M. papillorobustus* could represent a 'keystone parasite'.

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