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ALTERNATIVE REPRODUCTIVE STRATEGIES IN THE PROGENETIC TREMATODE *COITOCAECUM PARVUM*: COMPARISON OF SELFING AND MATING WORMS

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ABSTRACT: The progenetic opecoelid trematode *Coitocaecum parvum* can reproduce either precociously by selfing in its second intermediate amphipod host or by mating in its normal definitive fish host. In this study, we describe and compare the infection parameters and some life history traits of both egg-producing worms and non–egg producing worms in both their second intermediate and definitive hosts. We showed that 58% of worms start to produce eggs while still in the amphipod. The relative abundance of progenetic worms increased with amphipod size, and egg-producing worms achieved greater size in amphipods than in fish. These 2 findings support the reproductive insurance hypothesis. No difference in size was revealed between eggs produced in the amphipods and those produced in the fish. Although more information is needed to thoroughly assess the respective costs and benefits of selfing and mating in this species, our conclusion is that adopting progenesis may have few, if any, long-term negative consequences for the parasite.

Selfing, defined as the process of fusion of male and female sex cells produced by the same individual, is the most extreme case of inbreeding. It occurs in hermaphroditic plants and animals, whether male and female systems are sequentially or simultaneously functional (Jarne and Charlesworth, 1993; Thornhill, 1993).

Self-fertilization is however commonly associated with a major disadvantage, i.e., inbreeding depression (D. Charlesworth and B. Charlesworth, 1987). To some extent, selfing may be an evolutionary dead end because it may result in the loss of genetic diversity and consequently preclude adaptation to changing environments. Although the basic premise of selfing as a dead end is widely accepted, there have been few rigorous evaluations of the hypothesis (Thornhill, 1993; Weeks et al., 2001). Cross-fertilization, in contrast, produces more genetically heterogeneous offspring than does selfing, which may be particularly important in the arms race taking place in host–parasite systems (Hamilton, 1980; Bell and Maynard Smith, 1987; Lively, 1987).

Although in most species the breeding strategy (self-fertilization vs. cross-fertilization) is a fixed characteristic that persists through generations, in some cases the adoption of 1 of these 2 strategies is more flexible and facultative. For instance, hermaphroditic parasites may reproduce either alone by selfing or in pairs by outcrossing (Nollen, 1983).

Limited availability of mating partners has been proposed as an explanation for the occurrence of simultaneous hermaphroditism in animals with pair mating (Charnov et al., 1976; Christen and Milinski, 2003). When low population density or low mobility of individuals limits the number of potential mates, simultaneous hermaphrodites may have a selective advantage because: first, they are able to adjust the allocation of resources between male and female functions to maximize fitness; second, in a hermaphroditic population, the likelihood of meeting a partner is higher because all individuals are potential mates; third, in the absence of mating partners, many simultaneously hermaphroditic animals have the option of reproducing through self-fertilization. Hermaphrodites can thus be used as a model to study potential costs and benefits of selfing (Christen et al., 2002).

In this study, we used the opecoelid trematode *Coitocaecum parvum* (Crowcroft, 1945) as a model species (see Fig. 1 for details of the life cycle). This hermaphroditic parasite may reproduce by mating with a partner in the intestine of the definitive fish host (bullies, *Gobiomorphus* spp. or eels, *Anguilla* spp.) or by self-fertilization in the second intermediate host (crustaceans, mainly the amphipod *Paracalliope fluviatilis*) (MacFarlane, 1939; Holton, 1984a). This phenomenon of early reproduction, while still encysted in the intermediate host, is called progenesis (Dollfus, 1924; Gould, 1977). Both types of egg-producing worms, either in the amphipod or in the fish, clearly belong to the same species and do not correspond to genetically different strains (on the basis of comparisons of 16S mitochondrial DNA; K. Donald, pers. comm.). Therefore, rather than a fixed strategy, precocious reproduction by selfing in this species is a facultative strategy that seems to be driven by local environmental cues (Holton, 1984b; Poulin, 2001). Indeed, the proportion of trematodes adopting progenesis within amphipods may rise in the absence of chemical odors emanating from the fish host, or in case of low expected life span of the second intermediate amphipod host, or both (Poulin, 2003). Progenesis thus seems to be favored when the window of transmission opportunities to the definitive host is reduced.

The potential benefits of early reproduction in the second amphipod host appear to revolve around 2 key points. First, the subsequent reduction in the number of transmission events, the simpler life cycle being easier to complete. Second, the insurance of producing eggs without the risk of not finding a mate in the fish intestine, i.e., reproductive insurance. However, because progenesis may be achieved only through self-fertilization in this species (precocious adults are individually encysted within a metacercariae cyst), this inbreeding strategy is expected, at least hypothetically, to incur substantial costs.

In this study, we describe and compare morphological characteristics of both egg-producing and non–egg producing worms in both the second intermediate amphipod host and the definitive fish host. We intended to expose some life history traits that could be associated with each alternative strategy, a first essential step to assess the pros and cons of selfing progenesis.

MATERIALS AND METHODS

Sampling

Amphipods, *P. fluviatilis* (Amphipoda: Eusiridae), and fish, *Gobiomorphus cotidianus* (Perciformes: Eleotridae), were collected at the same

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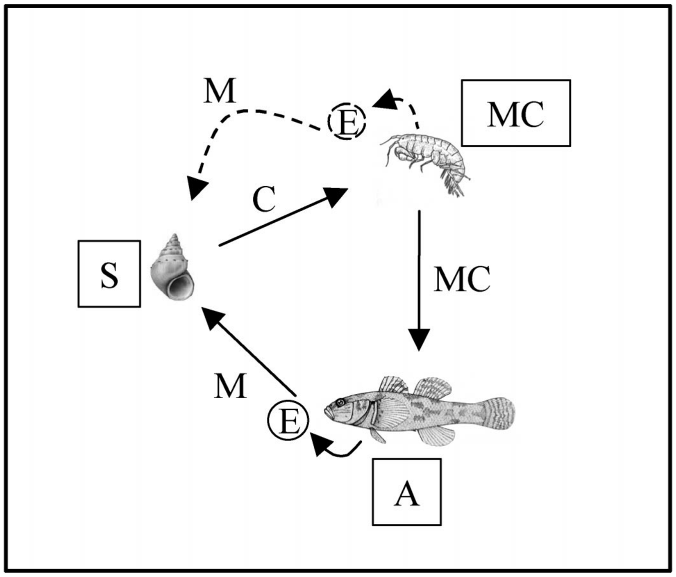

FIGURE 1. Life cycle of the trematode *Coitocaecum parvum*. Parasite stages that develop within the hosts are in rectangles; those that are transmitted between hosts are shown alongside the arrows. From the eggs (E) released with the faeces of fish (here, the common bully *Gobiomorphus cotidianus*), free-swimming miracidia (M) hatch and infect the snail *Potamopyrgus antipodarum*. In the first intermediate host, they develop as sporocysts (S) that produce cercariae (C). Cercariae leave the snail to infect and encyst as metacercariae (MC) in crustacean hosts (here, the amphipod *P. fluviatilis*). The life cycle is completed when the second intermediate host is ingested by the definitive fish host. In the fish intestine, they mature and become egg-producing adults (A). A simpler life cycle may be adopted by progenetic development: following encystment in the crustacean host, metacercariae develop precociously into an egg-producing worm (broken arrows).

place in a New Zealand lake (Lake Waihola, 40 km southwest of Dunedin, South Island, 46°01′S, 170°05′E). Samples were taken weekly, from 2 June to 28 July 2003 (for a total of 9 distinct samples). Amphipods were randomly collected by dragging a dip net through a patch of macrophytes (*Myriophyllum triphyllum*) at a distance of 5–10 m from the shore (mean depth of approximately 0.5 m). Bullies were individually caught with a dip net after displacing rocks they use as shelter alongside the shore (0–5 m from the shore, mean depth 0.25 m).

Animals were returned to the laboratory and maintained in aerated lake water. Strands of macrophytes were added as food for amphipods, and bullies were kept unfed to avoid any further infections. Dissections and examination for parasites of both amphipods and bullies were performed during the 4 days after the day of collection.

Parasite infection levels within the 2 hosts

All collected fish were considered without distinction for size. For amphipods, all individuals large enough for sex determination (according to the development of the second pair of gnathopods) were retained, meaning practically all animals longer than 1.5 mm.

Parasitological terminology applied throughout the article follows the recommendations of Bush et al. (1997). Because the prevalence of *C. parvum* was relatively low in amphipods (<5% according to previous investigations), it was not determined by dissection. Rather, an alternative method of prevalence estimation was applied as follows. Amphipods were screened under a binocular microscope to visually assess the presence of encysted metacercariae through the cuticle. Two groups were thus formed, i.e., 1 with amphipods judged as infected and 1 with amphipods judged as uninfected. A subsample of individuals was then dissected in each group to verify their actual infection status. Therefore, it was possible to calculate an assessment error of type 1 (amphipods judged as uninfected, whereas they were in fact infected) and an assessment error of type 2 (judged as infected, whereas not infected), these 2 values providing a confidence interval limit around the true prevalence. This noninvasive method was shown to be less time consuming and allowed large samples to be processed.

At dissection, amphipods were measured to the nearest 0.1 mm (total length from the anterior tip of the cephalon to the end of the uropods), sexed, and searched for parasites within the hemocoel. Bullies were measured to the nearest 1 mm (total length from the tip of the mouth to the end of the caudal fin), decapitated, sexed, and the whole digestive tract was removed to search for parasites. Two developmental stages of *C. parvum* were distinguished according to the presence or absence of eggs (either in utero or released into the metacercariae cyst) and thereafter referred to as non–egg producing worm or egg-producing worm.

Parasite life history traits

Parasite dimensions were taken to the nearest 0.025 mm by placing the worm in a drop of 70% alcohol and by measuring the total length and the largest width (at the level of the ventral sucker). These linear dimensions were then used to compute the surface area of each worm using the formula for the surface area of an ellipse: $S\ worm = \pi \times (L/2) \times (W/2)$, where L and W are the length and width, respectively.

For each egg-producing worm in amphipods, the total number of eggs released was counted and the length and the width of a subsample of 10 eggs was measured to the nearest 2.5 μm. All *C. parvum* worms found in fish were individually placed in a drop of lake water to induce them to release their eggs. In that case, the total number of eggs released was counted and measured to the nearest 2.5 μm. Assuming a regular ellipsoid shape, individual egg volume was then calculated as $V\ egg = (\pi \times L \times W^2)/6$. Throughout the article, parasite size and egg size now refer to surface and volume, respectively. Length and width values were not used further, unless specifically mentioned.

Data analysis

We made the assumptions that eggs produced by *C. parvum* worms in the amphipods resulted from self-fertilization (worms are individually enclosed within a cyst wall) and that eggs produced in the fish derived from cross-fertilization. Although the latter assumption may not always hold, i.e., selfing in the presence of mating partners in the fish, this would have a conservative effect on the results because it would act to reduce the difference between outcrossing and selfing and thus reduce our chance of finding significant differences.

Statistical analyses were performed following the recommendations of Sokal and Rohlf (1995). All tests were performed using the STATISTICA software (Statsoft Inc., Tulsa, Oklahoma, 2001, version 6). When conditions for using parametric statistics were violated, nonparametric statistical tests were used instead. In Mann–Whitney tests, *z* values were computed after correction for ties because many values were similar between groups. All means were given ±SE. All tests were 2-tailed, and *P* values were considered significant at the 5% level.

RESULTS

Parasite infection levels within the 2 hosts

In amphipods: Overall, 6,810 amphipods were screened individually using a binocular microscope for visual determination of infection status. The overall prevalence was estimated as 220/6,810 = 3.23%. After the dissection of a subsample of 223 amphipods judged as uninfected, the assessment error of type 1 was estimated as 12 × 100/223 = 5.38%. Similarly, after the dissection of a subsample of 71 amphipods judged as infected, the assessment error of type 2 was estimated as 21 × 100/71 = 29.58%. This high error value in the visual assessment of the infection status was mainly due to the confounding occurrence of another trematode (*Microphallus* sp.) that also encysted in the amphipod. Given these 2 assessment errors (29.58 and 5.38%), the confidence interval limit around the estimation of 220 infected amphipods was 154–575, meaning a prevalence value comprised between 2.26 and 8.44%.

Of the 220 amphipods among 6,810 visually classified as

TABLE I. Infection parameters of *Coitocaecum parvum* in the crustacean and the fish hosts.*

Host	Infection parameters	Non–egg-producing worms	Egg-producing worms	Both worm stages
Amphipod	Prevalence	—	—	3.23 (6,810)
	Intensity	1.40 ± 0.09 (70)	1.28 ± 0.05 (101)	1.68 ± 0.09 (136)
Bully	Prevalence	79.31 (29)	96.55 (29)	100.00 (29)
	Intensity	5.26 ± 0.89 (23)	5.50 ± 0.91 (28)	9.48 ± 1.61 (29)

* Prevalence in % and mean intensity ± SE are shown separately for the two developmental stages of the parasite, i.e., non–egg-producing worms and egg-producing worms. The number of host individuals examined to compute each infection parameter is given in parentheses. The total prevalence value in amphipods is an estimate, the true value lying between 2.26 and 8.44% (see Results).

infected, 163 were really infected by *C. parvum* (163 × 100/6,810 = 2.39%). Morphometric analyses were performed on 136 of these *C. parvum*–infected amphipods (the remaining infected amphipods were used in a predation experiment and were not further considered herein). Details on infection parameters in both amphipod and fish hosts are given in Table I. The intensity ranged from 1 to 6 parasites for a mean value of 1.68 ± 0.09. Males harbored more *C. parvum* than females, but the difference was not significant (Mann–Whitney *U*-tests: $P > 0.05$ for non–egg producing worms, egg-producing worms, and both types of worms). A significant difference in relative abundance was revealed between non–egg producing worms and egg-producing worms (0.72 ± 0.08 vs. 0.96 ± 0.06; Wilcoxon matched pairs test: $z = 2.26$, n = 136, $P < 0.05$). A significant positive relationship was found between amphipod size and parasite intensity, considering non–egg producing worms (Spearman rank order correlation: $r_S = 0.34$, n = 70, $P < 0.01$), egg-producing worms ($r_S = 0.31$, n = 101, $P < 0.01$), or both ($r_S = 0.40$, n = 136, $P < 0.001$). Host size was positively and significantly correlated with the relative abundance of non–egg producing worms (Spearman rank order correlation: $r_S = 0.17$, n = 136, $P < 0.05$), and the relationship was stronger with egg-producing worms ($r_S = 0.23$, n = 136, $P < 0.01$). Overall, the proportion of infected amphipods harboring progenetic worms was 101 × 100/136 = 74.26%.

In fish: All the 29 bullies examined were infected by *C. parvum*. The total number of parasites per host ranged from 2 to 33, with a mean intensity of 9.48 ± 1.61 (see Table I). There was no significant relationship between host size and parasite intensity (Spearman rank order correlation: $r_S = 0.13$, n = 29, $P = 0.52$). Parasite intensities were statistically similar between host sexes (Mann–Whitney *U*-tests: $P > 0.16$ for non–egg producing worms, egg-producing worms, and both types of worms).

No difference in prevalence was revealed between the 2 developmental stages of the parasite (Yates corrected chi-square test: $\chi^2 = 2.60$, df = 1, $P = 0.11$) and they did not differ in relative abundance either (4.17 ± 0.81 vs. 5.31 ± 0.90; Wilcoxon matched pairs test: $z = 1.87$, n = 29, $P = 0.06$). Overall, the proportion of fish harboring egg-producing worms was 28 × 100/29 = 96.55%.

Comparison between hosts: Prevalence of *C. parvum* was far lower in amphipods than in fish (2.39 vs. 100%). The same was observed for mean intensity (Mann–Whitney *U*-test: $z = 7.50$, $P < 0.001$), and this was true for non–egg producing worms (Mann–Whitney *U*-test: $z = 4.87$, $P < 0.001$) as well as egg-producing worms (Mann–Whitney *U*-test: $z = 6.77$, $P < 0.001$). Among infected hosts, the proportion of egg-producing worms was significantly higher in the fish than in amphipods (Yates corrected chi-square test: $\chi^2 = 5.72$, df = 1, $P < 0.001$).

Parasite life history traits

In amphipods: A proportion of 130 × 100/224 = 58.04% of all parasites were egg-producing worms (see Table II). Non–egg producing worms were significantly smaller than egg-producing worms (unpaired *t*-test: $t = 18.03$, df = 222, $P < 0.001$).

There was no relationship between host body size and individual size of parasites (Pearson correlation for non–egg producing worms: $r = 0.10$, n = 94, $P = 0.35$; for egg-producing worms: $r = -0.09$, n = 130, $P = 0.32$) or between host body size and mean parasite size within the host ($r = 0.09$, n = 135, $P = 0.31$).

For non–egg producing worms, there was no difference in

TABLE II. Body size dimensions of *Coitocaecum parvum* in the crustacean and the fish hosts.*

Host	Body dimensions	Non–egg-producing worms	Egg-producing worms	Both worm stages
Amphipod	n	94	130	224
	Length	0.6293 ± 0.0161	0.9150 ± 0.0120	0.7951 ± 0.0135
	Width	0.1891 ± 0.0063	0.3267 ± 0.0040	0.2690 ± 0.0058
	Surface	0.0984 ± 0.0051	0.2376 ± 0.0055	0.1792 ± 0.0060
Bully	n	121	154	275
	Length	0.8058 ± 0.0131	0.8971 ± 0.0107	0.8569 ± 0.0088
	Width	0.2500 ± 0.0056	0.2896 ± 0.0035	0.2722 ± 0.0033
	Surface	0.1635 ± 0.0060	0.2058 ± 0.0041	0.1872 ± 0.0037

* Values are presented as mean ± SE (linear dimensions [mm] and surface, assuming an ellipse shape [mm^2]).

individual body size with respect to the intensity of infection within the host, i.e., with the number of other worms sharing the host (analysis of variance [ANOVA]: $F_{5,88} = 1.08$, $P = 0.38$; analysis of covariance [ANCOVA] with host length as covariable: $F_{5,87} = 0.99$, $P = 0.43$). In contrast, for egg-producing worms, there was a significant difference in body size according to the number of other worms within the host (ANOVA: $F_{3,123} = 3.28$, $P < 0.05$; ANCOVA with host length as covariable: $F_{3,122} = 2.99$, $P < 0.05$). The body size of egg-producing worms increased as the intensity of infection rose (Spearman rank order correlation: $r_S = 0.22$, n = 127, $P < 0.05$). This may, at least, reflect an absence of competition for resources or space within the amphipod host.

The number of eggs in the cyst ranged from 3 to 501 for a mean number of 139.73 ± 13.64. There was a positive relationship between parasite size and the number of eggs they released (Spearman rank order correlation: $r_S = 0.33$, n = 85, $P < 0.01$). There was also a strong relationship between the number of eggs released in the cyst and the number of eggs still in utero (range from 0 to 9, mean number = 2.94 ± 0.19; $r_S = 0.30$, n = 85, $P < 0.01$).

In fish: Non–egg producing worms were significantly smaller than egg-producing worms (see Table II, unpaired *t*-test: $t = 6.03$, df = 273, $P < 0.001$). There was no relationship between host body length and individual size of parasites (Pearson correlation for non–egg producing worms: $r = 0.10$, n = 121, $P = 0.29$; for egg-producing worms: $r = -0.07$, n = 154, $P = 0.38$) or between host body length and mean parasite size within the host ($r = 0.18$, n = 29, $P = 0.36$).

During the time parasites were placed in a drop of lake water, 63 × 100/154 = 40.91% of the egg-producing worms released eggs (63 × 100/275 = 22.91% of the total parasites). Thus, more than half of the parasites, although harboring eggs in utero, did not release their eggs.

When released, eggs were not numerous (range from 1 to 8, mean number = 1.59 ± 0.14). There was a positive, although nonsignificant, relationship between parasite size and the number of eggs they released (Spearman rank order correlation: $r_S = 0.20$, n = 63, $P = 0.11$). There was a positive relationship between the number of released eggs by this in vitro technique and the total worm production, i.e., eggs released plus eggs still in utero ($r_S = 0.41$, n = 154, $P < 0.001$).

Comparison between hosts: The size frequency distribution of non–egg producing worms differed between the 2 hosts (see Fig. 2; Kolmogorov–Smirnov 2-samples test: $D_- = -0.45$, $D_+ = 0.00$, $P < 0.001$). The parasite size within the amphipods was significantly smaller than within the fish (unpaired *t*-test: $t = 8.00$, df = 13, $P < 0.001$). The smallest parasite found in amphipods was 0.2 mm long, whereas it was 0.4 mm in fish (see Fig. 3).

The smallest egg-producing worm was 0.60 mm long in amphipods and 0.45 mm in fish, which can be considered as the minimal reproductive size in this species. For both hosts, the largest size achieved by the parasite seemed to be a length of 1.3 mm (see Fig. 3). Between these minimal and maximal values for egg-producing worms, the size frequency distribution differed between the 2 hosts (see Fig. 2; Kolmogorov–Smirnov 2-samples test: $D_- = -0.01$, $D_+ = 0.26$, $P < 0.001$). Egg-producing parasites were on average larger in amphipods than in fish (unpaired *t*-test: $t = 4.76$, df = 282, $P < 0.001$). The length of eggs produced in amphipods was significantly higher than the length of those produced in fish (see Table III, ANOVA: $F_{1,134} = 6.94$, $P < 0.01$). In contrast, eggs produced in amphipods tended to be smaller in width, although the difference was not significant (ANOVA: $F_{1,134} = 3.73$, $P = 0.055$). As a result, with respect to egg volume, no difference was detected between self-fertilized eggs produced in amphipods and cross-fertilized ones produced in fish (ANOVA: $F_{1,134} = 0.13$, $P = 0.72$).

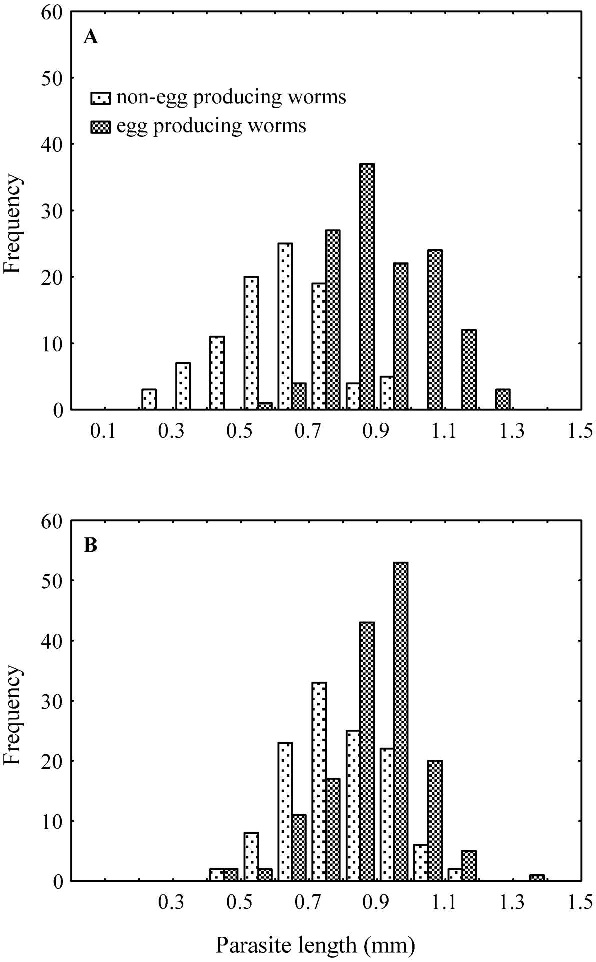

FIGURE 2. Size frequency distribution of non–egg producing worms and egg-producing worms. **A.** In the amphipod host. **B.** In the fish host.

DISCUSSION

As a general rule emerging from other host–parasite systems (e.g., Marcogliese, 1995), the prevalence in *C. parvum* increases with the host trophic levels. In this study, the prevalence was found to be lower than 10% in the second intermediate amphipod hosts, whereas it was 100% in the definitive fish hosts. Dissection of first intermediate snail hosts, *Potamopyrgus antipodarum*, from the same sampling site showed that the prevalence among first intermediate hosts was lower than 1% (data not shown).

Within amphipod hosts, 58% of all parasites started to produce eggs before reaching the definitive host in which reproduction normally occurs in this species, as well as in trematodes

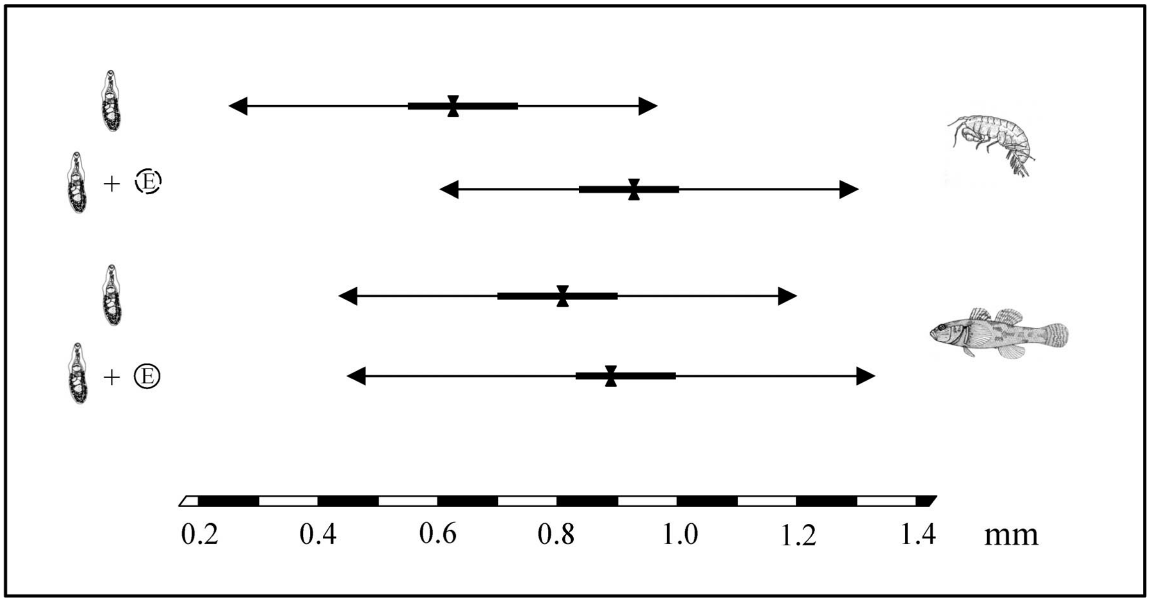

FIGURE 3. Length of egg-producing and non–egg producing worms in the crustacean and the fish hosts. Egg-producing worms are symbolized by +E. The range (within minimal and maximal values) is given between arrowheads (↔). Lower and upper quartiles are given by bold lines (—), and the position of the mean is indicated within the interquartile range.

in general. However, among those parasites within amphipods, a large proportion was still undergoing development and not mature enough to produce eggs, i.e., growing metacercariae. Taking the parasite reproductive size as the minimal size at which 1 parasite was found to lay eggs (here 0.6 mm in the amphipods, see Fig. 3 and Table II), the actual proportion of parasites reproducing early can be estimated at up to 66%. This could vary seasonally, although seasonal differences in water temperature and other environmental factors are not pronounced in southern New Zealand.

Why is such a high proportion of parasites choosing to reproduce early, without mating with a partner in the intestine of the fish host? Because *C. parvum* was found in nearly all bullies along the shoreline of Lake Waihola (100% prevalence in our sample) and because the mean intensity of infection is rather high (between 9 and 10 parasites per fish), the opportunities for cross-fertilization do not appear limited while in the fish. Pairs of copulating worms were occasionally observed during the short time of fish dissection (3 occurrences of copulation, 2.18% of total worms in fish). From our data, it is obvious that egg-producing worms in the amphipods are larger than their counterparts in the fish. The same observation was previously made by MacFarlane (1939). This is, in our view, strong evidence in favor of the reproductive insurance hypothesis (see Wang and Thomas, 2002). After spending some time in the amphipod, parasites start to reproduce because of the uncertainty of their transmission to a fish host before they die. In support, progenetic metacercariae were more frequent among larger, and older, amphipods. Time spent in the intermediate host is also believed to be an important trigger of progenesis in other trematodes (Poulin and Cribb, 2002).

TABLE III. Egg dimensions of *Coitocaecum parvum* in the crustacean and the fish hosts.*

Egg dimensions	Amphipod host	Bully host
n (n worms)	813 (85)	85 (51)
Length	73.925 ± 0.4623	72.016 ± 0.531
Width	44.118 ± 0.2816	45.006 ± 0.364
Volume	76.277 ± 1.240	76.993 ± 1.520

* Values are presented as mean ± SE (linear dimension [μm] and volume, assuming an ellipsoid shape $[\times 10^3\ \mu m^3]$).

Why then is there not a higher proportion of parasites reproducing while still in the amphipods? The common answer generally refers to the costs associated with selfing. In many systems indeed, self-fertilization is associated with disadvantages in comparison to cross-fertilization. In the cestode *Schistocephalus solidus*, selfers produced larger numbers of eggs, but these eggs were smaller and contained even smaller embryos per given egg size than eggs of potentially outbreeding cestodes. Selfed eggs achieved lower hatching rates, and outcrossed parasites had a higher infection success and a faster development in the host (Wedekind et al., 1998; Christen et al., 2002). Many other studies also demonstrated lower fitness for selfers in a wide range of organisms, i.e., in plants (Dudash, 1990), in snails (Jarne et al., 1991; Wethington and Dillon, 1997), and in nematodes (Prahlad et al., 2003). But there are also many investigations revealing no fitness costs associated with self-fertilization, i.e., in polychaetes (Hsieh, 1997), in snails (Doums et al., 1996), in monogeneans (Jackson and Tinsley, 1988), and in trematodes (Buttner, 1953; Nollen, 1971). For instance, in the trematode *Paralepoderma brumpti*, the definitive host is no longer necessary for completing the life cycle and, as recorded by Buttner (1953), the species did not lose its viability and showed no sign of degeneration even after 10 progenetic generations maintained in laboratory. To some authors, self-fertilization is even viewed as an adaptive strategy for the colonization of new areas (DozsaFarkas, 1995).

In the present system, no difference in egg size was observed between progenetic and normal parasites. However, more data are needed about egg viability and the lifetime fecundity of both types of parasites. Partial information is already available in the literature. Miracidia have been observed to hatch from eggs produced in amphipods (MacFarlane, 1939) and attempts to infect snails with progenetic eggs proved to be successful (at least to the sporocyst stage; Holton, 1984b). At present, the most likely explanation for the maintenance of selfing by progenesis in *C. parvum* is the unpredictability of transmission to the definitive fish host in which the parasite would normally find a partner and mate. Progenesis in this species must be viewed as a strategy of reproductive insurance. Furthermore, progenesis and selfing in the intermediate host probably do not preclude future cross-fertilization in the fish host, in the event that the amphipod host gets eaten by a fish.

In trematodes, progenesis occurs in many different families (Poulin and Cribb, 2002), but overall it is only known from a small minority of trematode species. If it can serve as an insurance against failed transmission to the definitive host, why is it not a more common life history strategy? One possible answer is that acquisition of resources from the second intermediate host, which must be necessary for accelerated growth and egg production, may not be possible in all trematodes because of the nature of their metacercarial cysts or their location in the host. Perhaps getting the eggs out of the intermediate host is not feasible in many systems. Whatever the reason, it is clear that progenesis, with all its apparent advantages, is not a common strategy.

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