Alternative life-history and transmission strategies in a parasite: first come, first served?

R. POULIN* *and* F. LEFEBVRE

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

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SUMMARY

Alternative transmission strategies are common in many parasitic organisms, often representing discrete phenotypes adopted in response to external cues. The facultative truncation of the normal 3-host life-cycle to a 2-host cycle in many trematodes provides an example: some individuals mature precociously, via progenesis, in their intermediate host and produce eggs without the need to reach a definitive host. The factors that determine how many and which individuals adopt the truncated life-cycle within a parasite population remain unknown. We investigated the occurrence of progenesis in the trematode *Stegodexamene anguillae* within its fish intermediate host. Location within the host was a key determinant of progenesis. Although the size and egg output of progenetic metacercariae encysted in host gonads did not differ from those of the few progenetic metacercariae in other host tissues, the likelihood of metacercariae becoming progenetic was much higher for those in the gonads than those elsewhere in the host. Progenetic parasites can only evacuate their eggs along with host eggs or sperm, providing a link between the parasite's transmission strategy and its location in the host. Host size and sex, and the presence of other parasite species in the host, did not affect the occurrence of progenesis in *S. anguillae*. However, the proportion of metacercariae in host gonads and the proportion of progenetic metacercariae both decreased with increasing numbers of *S. anguillae* per host. These results suggest that progenesis is adopted mostly by the parasites that successfully establish in host gonads. These are generally the first to infect a fish; subsequent arrivals settle in other tissues as the gonads quickly become saturated with parasites. In this system, the site of encystment within the fish host both promotes and constrains the adoption of a facultative, truncated life-cycle by the parasite.

Key words: complex life-cycle, *Gobiomorphus cotidianus*, progenesis, *Stegodexamene anguillae*, trematode.

INTRODUCTION

Phenotypic plasticity and rapid responses to selection in traits such as virulence or transmission strategy are hallmarks of many parasitic organisms (e.g. Bull, Molineux and Rice, 1991; Ebert and Mangin, 1997; Kaltz and Koella, 2003). In some parasite species, phenotypic plasticity may exist in the form of discrete alternative phenotypes. In such cases, the phenotype being expressed may represent an adaptive, state-dependent decision made by the developing parasite in response to extrinsic factors (Thomas *et al*. 2002). For instance, many taxa of parasitic worms with complex life-cycles display alternative transmission routes, which are generally shorter and simpler versions of their full complex life-cycle (Combes, 2001). This is particularly common among trematodes, where truncation of the life-cycle has been documented in over 80 species belonging to more than 20 different families (Poulin and Cribb, 2002; Lefebvre and Poulin, 2005*a*). Typically, life-cycle abbreviation in trematodes is facultative within a population, with some individuals truncating their life-cycle, and others that do not. The most common form of abbreviation involves progenesis, or the precocious sexual maturation of the worms inside their intermediate host, as opposed to the 'normal' phenotype in which maturity is only reached following transmission to the definitive host (Poulin and Cribb, 2002; Lefebvre and Poulin, 2005*a*).

If normal and truncated life-cycles are alternative phenotypes adopted via an adaptive state-dependent process, we would expect the choice of phenotype to follow external cues indicative of the fitness benefits associated with each phenotype (Thomas *et al*. 2002). For example, in the only study of the determinants of life-cycle strategies in trematodes, Poulin (2003) found that the trematode *Coitocaecum parvum* is more likely to adopt a truncated life-cycle in the absence of odours from its fish definitive host. The parasite matures precociously and produces eggs in its crustacean intermediate host when its opportunities for transmission to fish are limited, taking advantage of its crustacean host's ability to detect fish chemicals. The presence or absence of predator-induced stress responses in the intermediate host triggers a developmental switch in the parasite, leading either to the normal or truncated life-cycle (Poulin, 2003). It is not known whether such state-dependent developmental strategies exist in other trematodes.

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* Corresponding author. Tel: +64 3 479 7983. Fax: +64 3 479 7584. E-mail: robert.poulin@stonebow.otago.ac.nz

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Here, we investigate the influences of several external factors on the life-history and developmental strategies of another trematode, *Stegodexamene anguillae* (Lepocreadiidae). Adults of this common New Zealand trematode live in the intestine of eels, *Anguilla australis* and *A. dieffenbachii* (Macfarlane, 1951). Their eggs, released in eel faeces, hatch into free-swimming larvae that penetrate snails, in which they multiply asexually to produce cercariae, the next free-swimming infective stages. After being shed by snails, cercariae penetrate the skin of small fishes (families Eleotridae and Galaxiidae; Hine, Jones and Diggles, 2000). They then encyst as metacercariae in fish tissues, and await ingestion by an eel definitive host, where the worms will mature. This is the normal life-cycle, but Macfarlane (1951) has also found that some metacercariae grow larger than others and reach sexual maturity within their fish intermediate host; these progenetic metacercariae self-fertilize and release eggs within the metacercarial cyst. Holton (1984) has subsequently demonstrated that the eggs produced by progenetic *S. anguillae* are viable and hatch into larvae capable of infecting snail first intermediate hosts; progenesis thus allows the normal 3-host life-cycle to be truncated to a 2-host cycle.

What induces certain metacercariae to adopt progenesis and a truncated life-cycle? In theory, progenesis should only be used if the worm incurs greater fitness benefits from progenesis than from the normal life-cycle. As an insurance against the possibility of never reaching the definitive host, progenesis in the intermediate host should generally be favoured, unless it limits further reproduction once inside the definitive host (Poulin and Cribb, 2002). However, various factors may also constrain the options open to any given parasite. For instance, progenesis is associated with increased growth by the metacercariae. Growth rates and both the optimal and maximal size that a larval worm can achieve in its intermediate host are all usually negatively affected by the number of other worms in the host, whatever the mode of resource used by the parasites (Parker *et al.* 2003). Thus, intense competition among parasites may limit the number of worms that can achieve progenesis. This can be exacerbated by the need to be in a location within the host where the release of the eggs to the external habitat is possible. Macfarlane (1951) has noted that progenetic metacercariae of *S. anguillae* are often in the gonads of the host. This suggests that eggs may be passed out along with host sperm or eggs. Cysts of progenetic metacercariae are roughly the same diameter as fish eggs, and are released along with host eggs when female fish spawn (R. Poulin, personal observations). In a male fish, a whole metacercarial cyst could not possibly be released with host sperm, but the trematode's eggs could be released, following the rupture of the cyst; this mode of egg evacuation has not been confirmed, however. In any event, competition for limited space in host gonads could also constrain the adoption of progenesis as an alternative life-cycle.

Our objectives are to address the following specific questions regarding progenesis in the trematode *Stegodexamene anguillae*. (1) Is progenesis restricted to metacercariae in host gonads, or is this life-history strategy open to all metacercariae anywhere in the fish host? (2) Is the occurrence of progenesis influenced by host features and by the number of other parasites sharing the host with a given metacercaria? Answers to these questions will shed some light on the maintenance of these alternative strategies in the same parasite population.

MATERIALS AND METHODS

Common bullies, *Gobiomorphus cotidianus* (Eleotridae), were sampled outside the spawning season in Lake Waihola, just south of Dunedin, South Island, New Zealand. Fish were caught individually with a small dipnet among rocks close to the shore. They were returned live to the laboratory where they were measured (total length, mm), decapitated, sexed and dissected. The gonads of each fish were carefully removed, and all metacercariae found attached to or lodged inside the gonads of the fish host were recovered, identified and counted. The rest of the fish carcass was placed in a pepsin digestive solution (6 g pepsin and 7 ml of HCl in 1000 ml of water) for 24 h, to free the metacercariae located in other tissues. All metacercariae recovered after digestion were also identified and counted. Apart from *Stegodexamene anguillae*, most of the metacercariae belonged to *Telogaster opisthorchis*, a common parasite of bullies with the same 3-host life-cycle as *S. anguillae* (Macfarlane, 1945; Hine *et al.* 2000). Some metacercariae either belonged to an unknown species, or were damaged specimens of *T. opisthorchis*. All metacercariae that were not *S. anguillae* were pooled and are hereafter referred to as heterospecific metacercariae.

Each *S. anguillae* metacercaria was placed individually under a microscope. Its thin cyst was opened and the straightened worm was measured (total length) to the nearest 0·025 mm. About 1 worm in 5 could not be measured, because it had disintegrated within the cyst; these were apparently worms that had died recently prior to fish dissection, or that were damaged during dissection. Metacercariae of *S. anguillae* were classified as either 'normal' or progenetic, i.e. as without or with eggs. When progenetic metacercariae were encountered, the total number of eggs they had produced was counted; this included both the eggs released within the cyst and those still in utero.

All analyses were performed using parametric statistical tests. Data on worm length, numbers of parasites per fish and numbers of eggs per progenetic

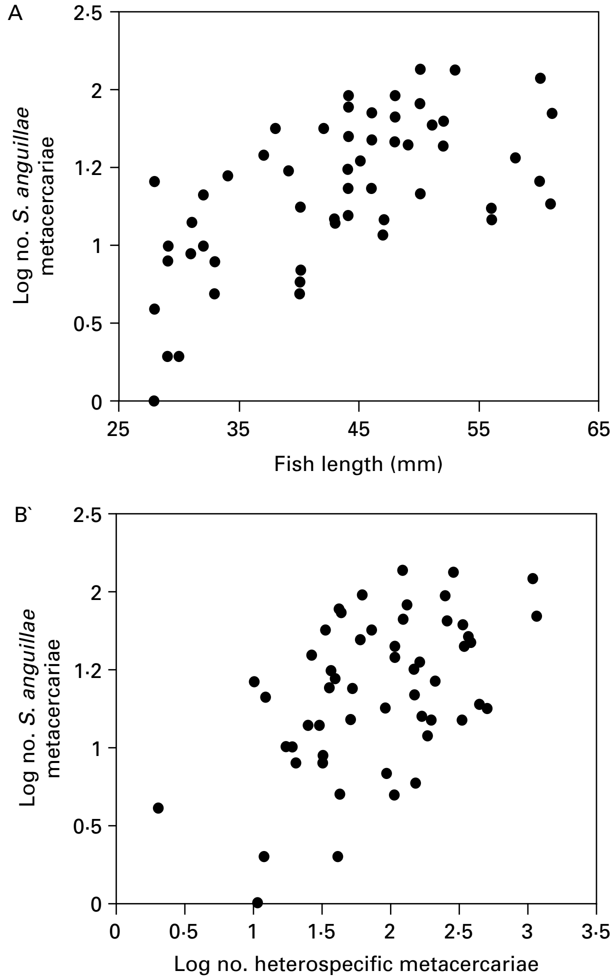

Fig. 1. Number of *Stegodexamene anguillae* in a fish as a function of (A) host fish length and (B) the number of metacercariae of other species in the same fish, across 54 individual fish.

worm were log-transformed (or log(x+1)-transformed, if there were zero values), whereas proportions, such as proportion of progenetic metacercariae per fish, were arcsine-transformed, even when untransformed data are shown in figures.

RESULTS

A total of 54 fish were investigated in this study. The fish included 28 females and 26 males, and ranged in length from 28 to 61 mm; males tended to be slightly longer than females ($t=1{\cdot}742$, D.F. $=52$, $P=0{\cdot}0875$). In addition to trematode metacercariae, all fish harboured low numbers (<25) of adults of the trematode *Coitocaecum parvum* in their gastrointestinal tract, and 3 fish had a single, unidentified nematode within a cyst in their body cavity, attached to the viscera. Preliminary analyses indicated that the presence of these parasites had no influence on the size of *Stegodexamene anguillae* metacercariae or the likelihood that they were progenetic, and they were therefore excluded from subsequent analyses.

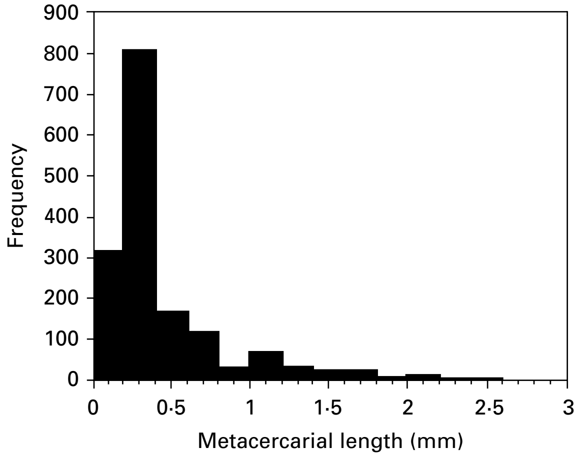

Fig. 2. Frequency distribution of worm lengths among 1645 metacercariae of *Stegodexamene anguillae* recovered from fish hosts.

In total, 2038 *S. anguillae* metacercariae (range 1–139 per fish) and 8801 heterospecific metacercariae (2–1147 per fish) were recovered. Only 152 (7·5%) of the 2038 *S. anguillae* metacercariae were progenetic, i.e. with well-formed eggs in utero or in their cyst. There was a clear positive correlation between fish length and the number of *S. anguillae* metacercariae per fish ($r=0{\cdot}626$, $N=54$, $P=0{\cdot}0001$; Fig. 1A). The number of heterospecific metacercariae per fish also correlated with fish length ($r=0{\cdot}852$, $N=54$, $P=0{\cdot}0001$), and thus, not surprisingly, there was a positive association between numbers of *S. anguillae* and heterospecific metacercariae ($r=0{\cdot}512$, $N=54$, $P=0{\cdot}0001$; Fig. 1B). There was no difference in numbers of *S. anguillae* or heterospecific metacercariae between male and female fish hosts (*t*-tests, both $P>0{\cdot}38$).

Only 1645 (80·7%) of the 2038 *S. anguillae* metacercariae recovered could be measured; these ranged in length from 0·075 to 3·0 mm. The majority were less than 0·5 mm long, but a second peak, though very small, in the length frequency distribution corresponds quite well to the appearance of progenetic metacercariae (Fig. 2). Roughly two-thirds of worms 1·0 mm or longer were progenetic. In a two-way ANOVA, worm length was not affected by its location within the host, i.e. either in the gonads or in other tissues ($F_{1,1641}=0{\cdot}072$, $P=0{\cdot}788$), but it was influenced by developmental strategy ($F_{1,1641}=385{\cdot}88$, $P=0{\cdot}0001$), with progenetic metacercariae being longer than normal ones (Fig. 3A). This difference may be even greater in reality, because many metacercariae with large numbers of eggs had disintegrated and could not be measured (see below). There was a weak interaction between worm location and developmental strategy ($F_{1,1641}=4{\cdot}72$, $P=0{\cdot}03$), such that the difference in size between progenetic and normal worms was slightly less pronounced if they were in the gonads (Fig. 3A). Across all fish hosts dissected, there were 521 *S. anguillae* metacercariae

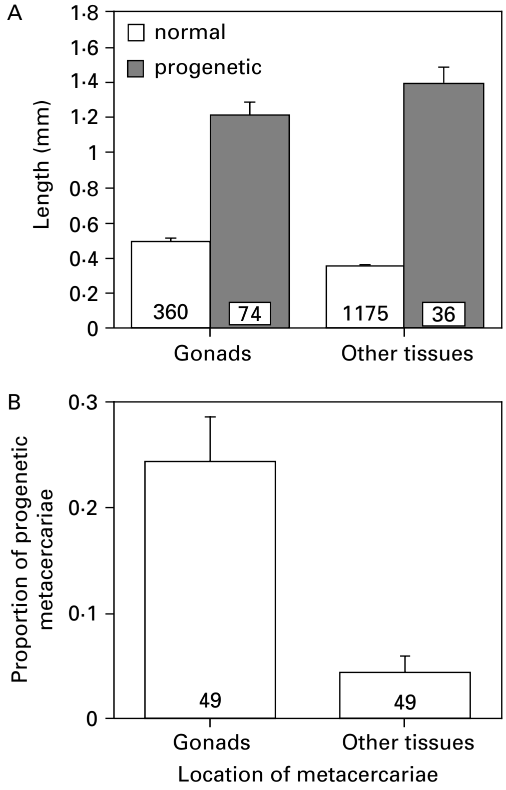

Fig. 3. (A) Mean (±S.E.) length of normal and progenetic metacercariae of *Stegodexamene anguillae* located in the gonads or other tissues in their fish hosts, and (B) mean (±S.E.) proportion of progenetic *S. anguillae* among all metacercariae found in either the gonads or other tissues of fish, including only fish in which there was at least 1 metacercaria in both the gonads and other tissues. Numbers at the base of columns indicate sample size.

found in the gonads, and 1517 found in other tissues. The proportion of progenetic metacercariae among those found in the gonads was much higher than among metacercariae found elsewhere in the fish's body (paired t-test using only fish with at least one *S. anguillae* metacercaria in both the gonads and elsewhere: $t=4{\cdot}97$, D.F. $=48$, $P=0{\cdot}0001$). Metacercariae in the gonads are more than 5 times as likely to be progenetic as those in other host tissues (Fig. 3B).

Among the 152 progenetic *S. anguillae* metacercariae recovered, the number of eggs per worm ranged from 5 to 1729, although the majority of metacercariae had fewer than 500 eggs (Fig. 4). Metacercarial cysts in which the progenetic worm had died and disintegrated contained significantly more eggs than those with a distinct and measurable worm (mean ± S.E.: 631 ± 62 eggs ($N=42$) versus 246 ± 25 eggs ($N=110$); $t=6{\cdot}246$, D.F. $=150$, $P=0{\cdot}0001$). For those progenetic metacercariae that could be measured, the number of eggs correlated positively with worm length ($r=0{\cdot}303$, $N=110$, $P=0{\cdot}0013$). Therefore, the residuals of the egg number versus worm length regression are used hereafter, to provide a measure of egg output corrected for body size. There was no difference in residual egg number between progenetic metacercariae in the gonads and those encysted in other tissues ($t=0{\cdot}383$, D.F. $=108$, $P=0{\cdot}703$).

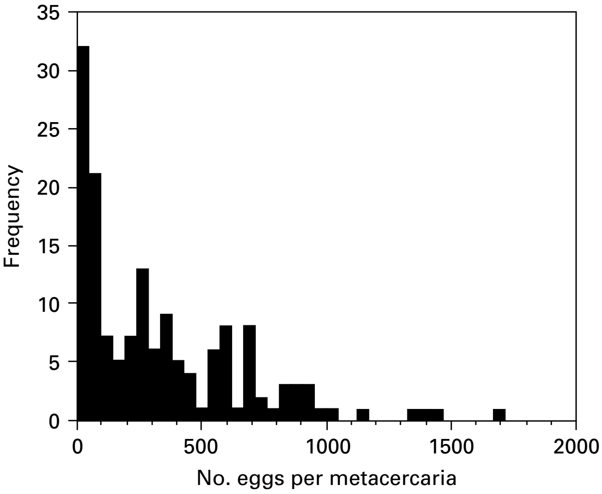

Fig. 4. Frequency distribution of numbers of eggs per worm, among the 152 progenetic metacercariae of *Stegodexamene anguillae* recovered from fish hosts.

To determine what factors affect the developmental strategy adopted by *S. anguillae* metacercariae across all 54 fish hosts, we looked at 4 dependent variables that are directly or indirectly associated with progenesis: the proportion of metacercariae that are located in the gonads, the proportion of progenetic metacercariae, average metacercarial size, and the residual number of eggs per worm. None of these variables is influenced by host sex (t-tests, all $P > 0{\cdot}19$). Each of the 4 dependent variables was used in a multiple regression testing for the separate effect of 3 predictor variables: fish length, the total number of *S. anguillae* metacercariae per fish, and the number of heterospecific metacercariae per fish. Neither fish length nor the number of heterospecific metacercariae was related to any of the 4 dependent variables (partial regression coefficients, all $P > 0{\cdot}28$). The total number of *S. anguillae* metacercariae per fish, however, had a marginal effect on the proportion of metacercariae in the gonads ($P=0{\cdot}0655$), and a stronger effect on both the proportion of progenetic metacercariae ($P=0{\cdot}0023$) and mean worm length ($P=0{\cdot}0051$). All 3 variables responded negatively to an increase in the total number of metacercariae (Fig. 5).

DISCUSSION

The complex life-cycle of trematodes involves a series of unlikely transmission events, and it is not surprising that selection has favoured reductions in the number of these transmission events (Poulin and Cribb, 2002). This is most frequently achieved by progenesis in the second intermediate host, with the definitive host not required for egg production (Lefebvre and Poulin, 2005*a*). In species like

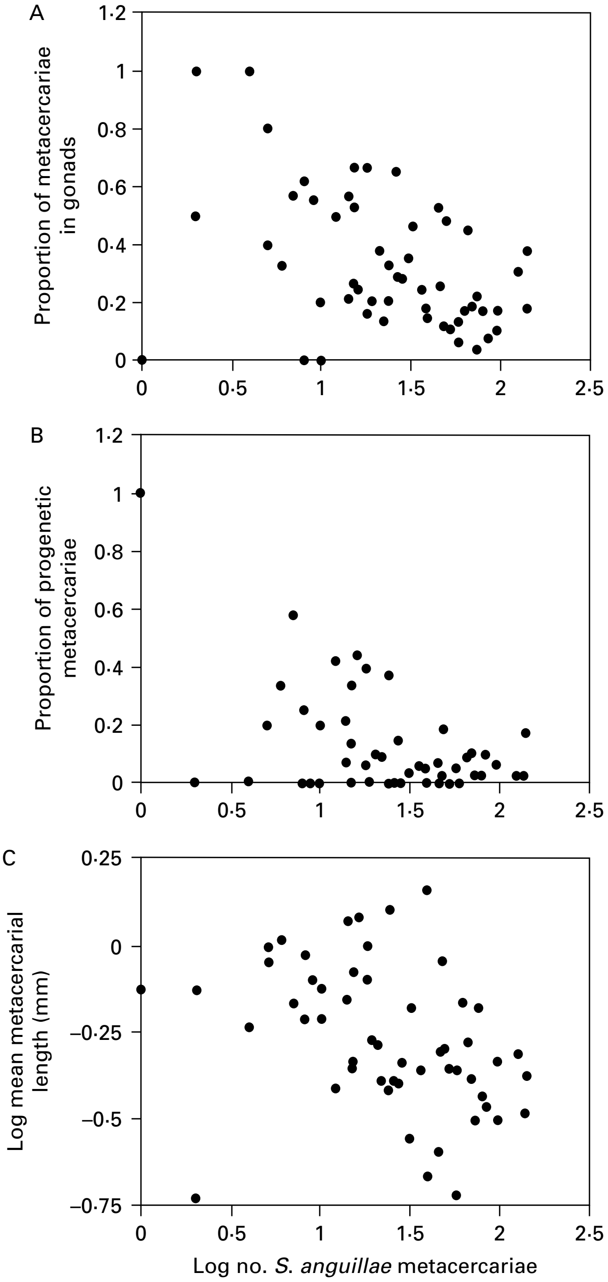

Fig. 5. Relationship between the number of *Stegodexamene anguillae* metacercariae in a fish host and (A) the proportion that are found in the gonads of fish, (B) the proportion that are progenetic, and (C) the mean length of the metacercariae, across 54 individual fish.

Stegodexamene anguillae, progenesis is facultative; there are thus 2 alternative phenotypes present in the population. However, the normal and progenetic phenotypes are not necessarily 2 discrete strategies; it could be that all metacercariae gradually progress towards progenesis. Here, we show a small discontinuity in the frequency distribution of worm lengths, creating a slight bimodality. This bimodality is very weak, but it corresponds to the appearance of progenetic individuals when worms are ranked from smallest to largest, a fact suggestive of 2 distinct life-history strategies: the 'normal' developmental route taken by most individuals, and progenesis adopted by only some individuals. Although this host-parasite system is not easily amenable to the kind of experimental investigations that would confirm our findings, we obtained strong observational evidence in answer to some basic questions regarding the determinants of these alternative strategies.

Firstly, the location of encystment within the fish intermediate host appears to matter. Normal metacercariae in host gonads are not larger than normal metacercariae found in other tissues, and progenetic metacercariae in gonads are also no different in size than those located elsewhere. However, metacercariae of *S. anguillae* inside host gonads are much more likely to be progenetic than those encysted elsewhere. One explanation would be that following penetration of the host, cercariae make an early decision between normal and progenetic strategies, with those opting for progenesis migrating to encyst in the gonads. An alternative explanation is that cercariae choose their encystment site more or less randomly, and that those ending up in the host gonads are then capable of switching to progenesis. In addition to providing an exit for the parasite's eggs, a location in the gonads may also provide the metacercariae with resources unavailable to parasites located in other host tissues. For instance, it may be easier in the gonads to divert from the host all the energy necessary for egg production. Nevertheless, those few progenetic metacercariae located outside the gonads achieve the same body length and relative fecundity as those inside the gonads. Whatever the explanation, location in the host gonads appears to be a key proximate explanation for the adoption of a progenetic life-history strategy in *S. anguillae*.

Secondly, the probability that a metacercaria is progenetic seems independent from host sex, host size or the number of metacercariae of other species present in the fish host. The only host-related variable related to the probability that any given *S. anguillae* metacercaria is progenetic was the total number of conspecific metacercariae in a fish. The negative relationship between average metacercarial size and number of *S. anguillae* metacercariae per host could represent a simple density-dependent competition for resources, as observed in other trematode species in their second intermediate host (e.g., Sandland and Goater, 2000; Brown *et al.* 2003). However, the fact that intensity of infection by *S. anguillae* also correlates negatively with the proportion of metacercariae in the gonads and the proportion of progenetic metacercariae suggests that any given fish can only sustain a finite number of progenetic parasites. Given the average size of a progenetic metacercarial cyst (about 1·3 mm diameter; Macfarlane, 1951) and the reduced size of host gonads in small fish (about 3 to 6 cm long) outside the reproductive season, there is only limited space in the gonads for these relatively large parasites. A likely scenario beginning with a small parasite-free fish is that metacercariae accumulate in the fish faster than the gonads can grow to accommodate additional metacercariae. Whether passively or by active site-selection, some of the first metacercariae to encyst in a fish will be lodged in the gonads. As more and more metacercariae accumulate, the gonads eventually become saturated with metacercariae, until a plateau is reached. We are not suggesting that the parasites have the cognitive ability or neuromuscular systems necessary to recognize that the gonads are saturated; the small size of fish gonads outside the reproductive season would simply prevent entry of further parasites once a certain number is reached. This would explain why both the proportion of metacercariae in the gonads and the proportion of progenetic metacercariae drop with increasing numbers of *S. anguillae* per fish. In fish harbouring fewer than 10 metacercariae of *S. anguillae*, 21% are progenetic; this number falls to 12% in fish with 10–50 metacercariae, and 5% in fish with more than 50 metacercariae. Whether the incoming cercariae actively compete for a place in the gonads, or whether their eventual location is determined passively, their chances of achieving progenesis depend to a great extent on their final destination. This suggests that the choice of life-history strategies by the parasite is more or less entirely constrained by the number of conspecifics in the host and how much space they leave for new parasites in the gonads: progenesis may be adopted on a first-come-first-served basis.

Once progenesis is adopted, eggs accumulate in the metacercarial cyst as the worm grows and keeps producing new eggs. Although most progenetic *S. anguillae* had only accumulated a few hundred eggs, some had well over a thousand. Our results suggest that after producing a few hundred eggs, a progenetic worm is likely to die; this is the only reasonable explanation for the larger number of eggs found in cysts containing disintegrated worms than in cysts with distinct worms. If still alive, progenetic worms may be capable of establishing as successfully as normal worms following their ingestion by definitive hosts, and carry on with egg reproduction. However, not only is the capture of a given bully by an eel a rather unlikely event, but also the establishment success of the metacercariae inside eels may be low. Field surveys indicate that in natural eel populations, between 26 and 78% of *Anguilla australis*, and 25 and 40% of *A. dieffenbachii*, are parasitized by adult *S. anguillae* in their gut, with typically about 8–10 worms per eel, on average (Rid, 1973; Hine, 1980). Individual bullies in the present study harboured on average 38 *S. anguillae* metacercariae; assuming that *S. anguillae* survives for up to 10 days inside an eel, then establishment success must be really low because eels eat several bullies per day (McDowall, 1990). Otherwise, even based on a conservative estimate of worm life-span, infection levels in eels should be much higher. Thus, as in other trematode species (Wang and Thomas, 2002; Lefebvre and Poulin, 2005*b*), progenesis can serve as a very effective insurance policy against failed transmission to definitive hosts. Indeed, progenetic *S. anguillae* occur in bullies from landlocked lakes from which eels are totally absent (Hine, 1978), and progenesis therefore can serve to maintain the life-cycle in the complete absence of the definitive hosts.

Of course, trematode fitness is not dependent only on the quantity of eggs produced and released, but also on their quality. Trematodes are hermaphrodites; within its cyst, a progenetic metacercaria can self-fertilize, but it cannot mate with another worm. This means that its offspring may suffer from inbreeding depression and reduced genetic diversity (Charlesworth and Charlesworth, 1987; Thornhill, 1993). For example, there is evidence from parasitic cestodes that the offspring of selfed worms are of lower quality than those of outcrossed worms, based on several fitness components (Wedekind, Strahm and Scharer, 1998; Christen, Kurtz and Milinski, 2002). Progenesis does not appear to have marked effects on the quality of trematode offspring (see Lefebvre and Poulin, 2005*b*; and review in Lefebvre and Poulin, 2005*a*), but there have been very few rigorous studies to date. We know that the eggs of progenetic *S. anguillae* are viable and hatch into functional infective larvae (Holton, 1984). However, we do not know whether these eggs achieve the same long-term success, i.e. rates of asexual multiplication in the snail host, etc. as those of normal adults cross-fertilizing each other in the intestine of eels. Therefore, the relatively high fecundity of progenetic metacercariae could be offset by lower offspring quality.

Alternative life-history and transmission strategies in parasitic organisms are more common than as presented in textbooks, where life-cycle diagrams suggest a single and inflexible transmission route. Elucidating what forces promote alternative phenotypes in parasites is important for our understanding of disease epidemiology and evolution. Studies on 2 progenetic trematodes illustrate that completely different factors may act on different species. In *Coitocaecum parvum*, progenesis in the second intermediate host is triggered by external signals related to the probability of reaching a definitive host (Poulin, 2003). In *Stegodexamene anguillae*, progenesis is adopted by metacercariae that succeed at encysting in host gonads (this study). These results emphasize that there is no single, common factor driving the evolution of transmission strategies of all parasites, even within 1 taxon of parasites.

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