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Tenure of individual larval trematode infections in an estuarine gastropod

Lawrence A. Curtis*

University Parallel Program, Department of Biological Sciences, and Graduate College of Marine Studies, University of Delaware, Newark, Delaware 19716, USA. *Correspondence address: Cape Henlopen Laboratory, College of Marine Studies, University of Delaware, Lewes, Delaware 19958, USA. E-mail: lcurtis@udel.edu

Ilyanassa obsoleta (Mollusca: Gastropoda) is an abundant inhabitant of salt marshes and tidal flats on the east coast of North America. Populations of this snail may be heavily infected by larval trematodes. Three species were observed in this work, *Himasthla quissetensis*, *Lepocreadium setiferoides*, and *Zoogonus rubellus*. Mostly as single-species infections, all occupy snail tissues as parthenitae that produce cercariae, which are released from the snail to infect the next host. By periodically testing snails for cercarial emission, single-species infections are here shown to persist over six summers and double-species infections are also noted to be long-lived. Among the 32 snails followed, 25 released the same (or no) cercariae throughout observation periods averaging three years. The other seven indicated infection changes, but only two of these are judged to reflect actual changes. The probability that a snail changed infection status in this study is thus 2.1% y^{-1}. *Ilyanassa obsoleta* individuals, and apparently their trematode infections, can persist for decades. Because species colonize and get evicted infrequently, sets of trematode species infecting *I. obsoleta* individuals (infracommunities) are concluded to be isolationist in character.

INTRODUCTION

Ilyanassa obsoleta (Say) is an estuarine neogastropod native to the east coast of North America. At least nine species of larval trematodes use this snail as first intermediate host and some populations are heavily infected (Curtis, 1997). Infected snails are sterilized and their growth rate is very much slowed (Curtis & Hurd, 1983; Curtis, 1995; Curtis et al., 2000). Infections are documented to persist for three summers (Curtis & Tanner, 1999). The results of tracking the trematode infections of individual *I. obsoleta* in the field for up to six summers are reported here. Results indicate that infections in this snail persist for many years mostly unchallenged by other infecting species.

In marine and estuarine environments, larval trematodes and their gastropod hosts are thought to have important ecological effects (e.g. Curtis & Hurd, 1983; Lauckner, 1987; Sousa, 1991; Rohde, 1993; Thomas et al., 1997; Mouritsen & Poulin, 2002). The extent of these effects depends partly on host longevity. Many marine snails live only 1–3 y [e.g. *Hydrobia ulvae* (Gorbushin, 1997) and, around England, *Littorina obtusata*, and *L. fabalis* (Williams & Brailsford, 1998)]. *Ilyanassa obsoleta* individuals stand to have lasting ecological effects because their longevity is extensive, reaching 30–40 y or more (Curtis, 1995; Curtis et al., 2000).

Parasite populations and communities are nested within individual hosts, host populations, and whole systems of hosts (Bush et al., 1997). The set of species infecting a host population is termed a component community and all parasite stages infecting all hosts in an ecosystem a compound community. Of most direct concern here is the infracommunity, the species infecting an individual host. In snail hosts the vast majority of trematode infections are by a single species, but as many as four can coexist (Esch et al., 2001). Holmes (1987) distinguishes between interactive and isolationist infracommunities. An interactive community is mainly characterized by species entering and leaving frequently. A trematode species would enter a snail as a colonizing miracidium (from a vertebrate definitive host) and potentially leave when evicted by antagonism from another colonizer. In an isolationist infracommunity colonizations and evictions are infrequent and established infecting species would typically persist unchallenged by colonizers. This distinction bears on whether infracommunities (and ultimately component communities) are structured by competition. There has been considerable debate on this issue (Esch et al., 2001; Hendrickson & Curtis, 2002).

Whether infections persist long, unchallenged by colonizing species, is directly pertinent to whether parasite infracommunities are interactive or isolationist. In snails, the history of individual infections can be followed. Infections consist of sporocysts and/or rediae that produce cercariae, which leave the snail to infect the next hosts. If a uniquely marked snail emits cercariae of all infecting species when tested initially, it can later be recaptured, and emits cercariae of all infecting species when retested, infection history can be followed without error. However, infecting species may fail to emit cercariae and possible errors must be considered (Curtis & Hubbard, 1990).

MATERIALS AND METHODS

The study site was the Savages Ditch area of south-eastern Rehoboth Bay, Delaware, USA (38°37′44″N

75°04′21″W). Snails live on a muddy to sandy bottom bordered by salt marsh. The water is shallow with a tidal depth ranging from emerged to about 1 m. The area is further described in Curtis et al. (2000).

Two groups of marked snails were used in this work. The first (N=231) was reported upon earlier by Curtis & Tanner (1999). A fuller account of the collection, size measurement, marking, release, and relocation of these snails is given by them. Briefly, snails were collected from an area, the 'Funnel' (Curtis et al., 2000), where snails tend to be large and trematode-infected. In the laboratory, snails were marked individually and initial shell heights measured. Initial infection status was determined by cercarial release: snails were placed in cups of seawater to see what species of cercariae, if any, would be emitted. Snails were released at a single location on 13 June 1996 and subsequent searches of the area were made at low-water to relocate marked snails. Curtis & Tanner (1999) give the infection histories of 35 snails in this group from 1996 into 1998 (their table V). Some of these snails were found in 1999–2001 and these provide extensions of infection histories. On finding a snail, its size was measured and a cercarial release test performed ($\geqslant$24 h duration). The mark was repaired as necessary and the snail re-released where found, usually within 2–3 days.

The other group of snails (N=500) was released in June of 1999. Groups of 100 marked *Ilyanassa obsoleta* were released at five locations in the area. Prior to release, numbered tags were applied to snails and shell apexes were painted with a blue fingernail varnish (to contrast with the red on 1996 releases). Initial shell height measurements and results of cercarial release tests ($\geqslant$24 h) were recorded. From 1999 to 2003, the time specifically covered in this report, 117 searches were made of the Savages Ditch area. Some of the 1999-released snails were recaptured, measured, and retested for cercariae during this time. They provide additional long-term histories of parasitism and growth in individual snails.

Finding marked snails was always a challenge. In 2002 only a few 1999, and no 1996, snails could be found. Snails had been free in the field from four to seven summers by this time, they were much scattered, and very few had bright (recently repaired) marks. The major problem was that nearly all snails were covered with a coating of mud and algal growth. Marks were utterly hidden by this and could not be detected at a distance. From March 2002 onward many snails were picked up and scraped off, but only a few 1999 marks were found this way.

RESULTS

Ilyanassa obsoleta (N=32) were tracked for up to six summers and tested a total of 107 times for release of cercariae. Three trematode species were encountered, *Himasthla quissetensis*, *Lepocreadium setiferoides*, and *Zoogonus rubellus* [see Curtis (2002) for taxonomic authorities]. Of snails released in 1996, 14 were observed for infection status and growth (Table 1). Curtis & Tanner (1999) reported upon all these snails (save 411) for the 1996–1998 period. For the sake of continuity and completeness, the same identifier numbers have been used and the previous observations included. Infections existed for long periods unchanged. All but one snail produced cercariae of the same species for the 4–6 y (spring–autumn search seasons) of observation (total snail-days=19,236). This result is supported by additional cercarial release tests done on some of these snails (Table 1). The 13 consistently parasitized snails grew very slowly (mean=0.2 mm 1 y^{-1}, range=0.1–0.4) [snail growth y^{-1}=(net shell height change/total elapsed days)×365]. Snail 458 (Table 1) released no cercariae initially, but later released *Lepocreadium setiferoides*. The infection could have been present initially, failing to release cercariae at testing, or

Table 1. *Trematode infection and growth histories of* Ilyanassa obsoleta *individuals at Savages Ditch (Rehoboth Bay, Delaware) between 1996–2001. Cercariae shed at various times (day/month) in each year are indicated. Snails were originally released on 13 June 1996 (505 was released on 25 October). Initial and final shell heights (mm) are given in parentheses. If different than last cercariae test, date of last measurement is given.*

Snail	1996	1997	1998	1999	2000	2001	
458	no (27.8)	–	*Ls* 03/06	*Ls* 26/04	–	–	(29.2, 09/05/1999)
279	*Hq* (29.9)	*Hq* 15/06	*Hq* 05/06	*Hq* 24/06	–	–	(30.1)
304	*Hq* (30.3)	–	*Hq* 11/06	*Hq* 06/10	–	–	(31.0)
324	*Hq* (28.9)	*Hq* 26/06	*Hq* 09/06	*Hq* 26/04	*Hq* 08/09	*Hq* 03/06	(29.5, 15/07/2001)
408	*Hq* (26.1)	–	*Hq* 05/06	*Hq* 12/07	–	–	(26.4, 09/08/1999)
441	*Hq* (30.1)	–	*Hq* 05/06	*Hq* 01/10	*Hq* 06/10	*Hq* 05/06	(31.2, 15/07/2001)
446	*Hq* (26.0)	*Hq* 14/09	*Hq* 01/06	*Hq* 19/06	–	*Hq* 01/06	(27.7)
460	*Hq* (27.3)	*Hq* 15/06	*Hq* 05/06	*Hq* 29/04	–	–	(28.2)
471	*Hq* (26.7)	–	*Hq* 28/10	*Hq* 20/09	*Hq* 12/05	–	(27.1)
505	*Hq* (27.4)	–	*Hq* 29/06	*Hq* 26/09	*Hq* 06/08	–	(28.8)
419	*Ls* (25.3)	–	*Ls* 30/09	*Ls* 27/09	*Ls* 08/09	–	(25.7, 06/10/2000)
492	*Ls* (29.2)	–	*Ls* 09/06	*Ls* 24/09	–	–	(30.0, 30/10/1999)
277	*Zr* (26.6)	–	*Zr* 13/07	*Zr* 05/12	*Zr* 04/11	*Zr* 23/07	(27.1)
411	*Zr* (29.1)	–	–	*Zr* 26/09	–	*Zr* 02/08	(29.4)

Symbols and abbreviations: –, not found; no, no cercariae released; *Hq*, *Himasthla quissetensis* cercariae released; *Ls*, *Lepocreadium setiferoides* released; *Zr*, *Zoogonus rubellus* released. Additional cercariae tests performed (d/month/y) are: snail 277, on 07/06/98, released *Zr* cercariae; 324, 03/06/01, *Hq*; 411, 27/05/99, *Zr*; 419, 12/07/99, 26/05/00, *Ls*; 441, 26/04/99, *Hq*; 471, 22/06/1999, *Hq*; 492, 29/04/99, *Ls*; and 505, 29/04/02, *Hq*.

Table 2. *Trematode infection and growth histories of* Ilyanassa obsoleta *individuals at Savages Ditch (Rehoboth Bay, Delaware) during 1999–2002. Cercariae shed at various times (day/month) in each year are indicated. YB snails were released in 1999 on 7 June, WB snails on 10 June, and BB snails on 19 June. Initial and final shell heights (mm) are given in parentheses. If different than last cercariae test, date of last measurement is given.*

Snail	1999	2000	2001	2002	
YB14	no (28.5)	–	*Hq* 03/06	–	(28.5, 15/06/2001)
WB24	no (29.7)	–	–	*Ls* 10/06	(30.7)
WB49	no (28.1)	–	*Hq* 02/08	–	(28.2)
BB39	no (27.2)	–	*Hq* 12/10	–	(27.7)
BB60	no (25.3)	–	–	no 24/06	(25.8)
YB11	*Hq* (28.1)	–	*Hq* 12/10	–	(27.8)
YB27	*Hq* (26.5)	–	*Hq* 23/04	–	(26.4)
YB39	*Hq* (30.2)	–	*HZ* 12/10	*HZ* 10/06	(30.6)
YB47	*Hq* (32.8)	*Hq* 24/09	–	*Hq* 02/06	(32.9)
YB49	*Hq* (28.7)	no 07/10	–	–	(28.8)
BB9*	*Hq* (26.1)	–	*Hq* 28/09	–	(26.2)
BB29	*Hq* (31.5)	–	*Hq* 12/10	–	(31.5)
BB57	*Hq* (29.6)	–	*Hq* 01/06	–	(29.5, 15/07/2001)
WB17	*Zr* (26.3)	–	–	*Zr* 26/06	(26.5)
BB5	*Zr* (29.7)	–	*Zr* 31/07	–	(30.3)
BB22	*Zr* (26.9)	–	*Zr* 28/09	–	(29.1, 12/10/2000)
BB40	*Zr* (24.9)	*Zr* 08/06	–	–	(25.1, 03/09/2000)
BB23	*LZ* (27.3)	–	*LZ* 23/04	–	(27.5)

Symbols and abbreviations are as in Table 1 except *HZ*, *Hq* and *Zr* cercariae released; *LZ*, *Ls* and *Zr* released. Additional tests are: YB39 on 20/06/01 produced *Hq* and *Zr* cercariae; YB47, 15/03/02, *Hq*; and BB9, 03/06/01, *Hq*. (*, also collected 02/04/03, elapsed days=1383, it released *Hq* cercariae and measured 26.3 mm).

the snail could have been newly colonized. In either case, the infection persisted for at least two summers once detected.

Snails released in 1999 (Table 2) were also initially quite large. Unlike 1996 snails, most were not initially collected in the Funnel. 'BB' snails (Table 2) came from the Funnel (except BB57 and BB60) and were released there. Other groups were collected and released outside the Funnel, where even larger snails can be initially uninfected (Curtis et al., 2000). Of the 18 snails, 12 demonstrated no change in infection status (total snail-days=10,424); BB60 released no cercariae and 11 others released the same species of cercariae throughout. Notably, one harboured two species, *Lepocreadium setiferoides* and *Zoogonus rubellus*, over three summers. Additional tests on some of these 12 snails (Table 2) support their unchanged infections. Among remaining snails, four did not release cercariae initially, but did in later tests. Two others appeared to either add (YB39) or lose (YB49) an infecting species. These six cases could be failures to emit cercariae at testing or actual infection changes. Among the 17 snails in Table 2, that at some point demonstrated infections, growth was typically slow (mean=0.1 mm y^{-1}, range= −0.1–0.9).

DISCUSSION

It is clear that individual trematode infections in *Ilyanassa obsoleta* can persist for many years. Of 32 snails tracked in this work, 25 showed no infection status change over observation times of 2–6 y (total snail-days=29,660). It is unlikely that the observed constancy results from miracidia of different species constantly attempting, but failing, to colonize. There is considerable evidence (Curtis, 1996, 1997; Curtis & Tanner, 1999) that the colonization rate of uninfected *I. obsoleta* by miracidia is low and existing infections appear to go mostly unchallenged.

Data on infections with two species are instructive. Hendrickson & Curtis (2002) studied *Himasthla quissetensis–Zoogonus rubellus* infracommunities. In these only *Z. rubellus* infrapopulations had reduced numbers, but they showed no sign of being evicted. In the field this double infection can persist for a long time: snail YB39 (Table 2) was observed to carry it for at least 355 d; and snail 267 in Curtis & Tanner (1999, table V) carried it for at least 728 d. Also, snail BB23 (Table 2), had a *Lepocreadium setiferoides–Z. rubellus* infection that persisted for at least 674 d. The host snail is presumably a limiting resource and competition between species infecting the same snail is often postulated. In sporocyst–rediae combinations, such as the above, rediae should dominate (e.g. Lim & Heyneman, 1972; Kuris, 1990). If a species-evicting process was occurring in these snails, it was proceeding at a slow, unobservable, pace.

Ultimately, it is not possible to know what happened with the seven snails that showed changes in released cercariae. Alternative scenarios may apply, but it is possible that two of them represent real changes. Snail 458 (Table 1) appeared to gain a *Lepocreadium setiferoides* infection between 1996 and 1998. Most (71%) of its total growth occurred in that period, and because parasitized snails grow slowly (Curtis, 1995; Curtis et al., 2000; this study), this snail probably gained the infection shortly before 1998. Snail WB24 (Table 2) originated outside the Funnel, where it stood a chance of being initially uninfected. After 1096 d of freedom it demonstrated an infection. Its 1.0 mm of growth makes it possible that this is another recently colonized snail. It was assumed that the other five [YB14, WB49, BB39, YB39, YB49 (Table 2)] to result from failures to emit cercariae from possessed infections.

Methodological uncertainties prompt the above speculations. Possibly, snails identified as persistently singly infected actually harboured unrevealed species, but this becomes unlikely when the same cercariae are released repeatedly. Prevalence of infected snails can be very high at Savages Ditch (Curtis, 1997) and infections must form sometime. The 32 snails in Tables 1 and 2 were free, between being initially and finally tested for cercariae, a mean of 1095 d (3.0 y). If two changed infection status, this gives a colonization rate of 2.1% y^{-1}. If all seven actually changed infection status, which is most unlikely, the rate would still be only 7.3% y^{-1}. Even at this rate, on average more than 10 y would pass before an infracommunity changed composition (Curtis & Tanner, 1999).

If the main feature of interactive communities is rapid colonization leading to a balance of species entering and leaving, then trematode infracommunities in *I. obsoleta* do not appear interactive. The majority of infections are single infrapopulations of sporocysts or rediae and their cercariae. Even though multiple-species infections in *I. obsoleta* are relatively common (Curtis, 1997), it is unlikely that parasite species encounter one another regularly (Curtis & Hubbard, 1993; Curtis, 2002). From this study, the evident pattern is one of long-lived infrapopulations that are rarely challenged for their snail host. Further, if challenged, they seem to coexist with the challenger (Hendrickson & Curtis, 2002) for extended durations, perhaps permanently. Following Holmes (1987), these infracommunities must be considered isolationist.

If a trematode manages to colonize a host snail, it would be maladaptive to relinquish it because probability of being transmitted, through other hosts in the life cycle, back to another snail is slight. Dronen (1978), as cited by Bush et al. (2001, p. 351), provided data to calculate the very small probability for a freshwater trematode. Data do not exist to estimate this for any marine trematode, but considering alone the small chance of colonizing the next snail, the probability of life cycle completion for an infrapopulation in *I. obsoleta* must be similarly small. Long residence in a snail, even if with another species, and the resulting extended production of cercariae would help counter this low probability of success.

Curtis (2002) considered three marine gastropod–trematode systems, those of *Ilyanassa obsoleta*, *Cerithidea californica*, and *Littorina littorea*. In the latter two systems as well, trematode colonization rate appears to be low, the host is long-lived, and infections persist long (Rothschild, 1942; Sousa, 1983, 1993). Certain trematode species are unable to coexist in all three hosts [*Himasthla quissetensis*–*Lepocreadium setiferoides* is such a pair in *I. obsoleta* (Vernberg et al., 1969; Curtis & Hubbard, 1993)]. This draws attention, but is not the basis of interactive infracommunities; rather, a substantial colonization rate by miracidia and short-lived infections because of evictions, must be shown. Sousa (1990, 1993) wisely noted that there are always new snails to infect in a reproducing snail population and trematodes can coexist in the component community even if not in infracommunities. This factor, coupled with a low colonization rate, makes interactive infracommunities unlikely, especially in long-lived snails. Trematodes are likely adapted to prolonged host longevity with a prolonged longevity of their own. One can imagine long-lived infections evicted slowly by accumulating colonizers, but this would be unobservable by any present method. The likelihood is that interactive larval trematode infracommunities will be discovered, if at all, among shorter-lived host snails. More data on colonization rates and infection longevities in a variety of snail hosts are needed.

Curtis et al. (2000) suggested that infections in *Ilyanassa obsoleta* are immortal within the life span of the host, which possibly extends to 60–70 y. Observing infections for six summers does not unambiguously demonstrate infection immortality. It is, however, virtually certain that the snails followed here did not have infections and shed cercariae only on occasions of being collected and tested. Infections were undoubtedly there and shedding cercariae long before, and will be long after, being observed.

In Delaware habitats *Ilyanassa obsoleta* individuals rarely reach 30 mm, but at Savages Ditch 35–39 mm snails regularly occur. Unless growth rates mislead, such snails are 50–70 y old and they have almost certainly been infected since they were about 30 mm and 30 y old (Curtis et al., 2000). Such individuals have exerted the ecological effects of snails for their entire time and, for the last 20–40 y or so, they have emitted cercariae that have infected second intermediate and ultimately definitive hosts. In marine systems particularly, we are largely ignorant of the ecological effects of parasites on hosts (Rohde, 1993), but the whole estuarine system stands to be shaped by the network of effects pondered here. Such an aged, complex system of hosts and parasites is irreplaceable in any practical time-frame and, even lacking a full understanding, it might be wise to take this into account and adopt a long-term, broad-scale perspective when thinking about parasites in marine and estuarine systems.

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