Ecology of larval trematodes in three marine gastropods

L. A. CURTIS*

University Parallel Program, Department of Biological Sciences and College of Marine Studies, University of Delaware, Newark, DE 19711 U.S.A.

SUMMARY

To comprehend natural host–parasite systems, ecological knowledge of both hosts and parasites is critical. Here I present a view of marine systems based on the snail *Ilyanassa obsoleta* and its trematodes. This system is reviewed and two others, those of the snails *Cerithidea californica* and *Littorina littorea*, are then summarized and compared. Trematodes can profoundly affect the physiology, behaviour and spatial distribution of hosts. Studying these systems is challenging because trematodes are often embedded in host populations in unappreciated ways. Trematode prevalence is variable, but can be high in populations of all three hosts. Conditions under which single- and multiple-species infections can accumulate are considered. Adaptive relations between species are likely the most important and potentials for adaptation of parasites to hosts, hosts to parasites, and parasites to other parasites are also considered. Even if colonization rate is low, a snail population can develop high trematode prevalence, if infections persist long and the host is long-lived and abundant. Trematodes must be adapted to use their snail hosts. However, both *I. obsoleta* and *L. littorea* possess highly dispersed planktonic larvae and trematode prevalence is variable among snail populations. Host adaptation to specific infections, or even to trematodes in general, is unlikely because routine exposure to trematodes is improbable. Crawl-away juveniles of *C. californica* make adaptation to trematodes in that system a possibility. Trematode species in all three systems are not likely adapted to each other. Multiple-species infections are rare and definitive hosts scatter parasite eggs among snail populations with variable prevalences. Routine co-occurrence of trematodes in snails is thus unlikely. Adaptations of these larval trematodes to inhabit the snail host must, then, be the basis for what happens when they do co-occur.

Key words: Gastropod, trematode, *Ilyanassa obsoleta*, *Cerithidea californica*, *Littorina littorea*.

INTRODUCTION

Studies from an ecological or evolutionary perspective on larval trematodes in marine molluscs have become numerous in recent years. The attention to marine systems is useful. Molluscs contribute much and are central in trematode life cycles. The impact of trematodes on the ecology of molluscan hosts can be very great and must not be underestimated (Curtis & Hurd, 1983; Lauckner, 1987; Sousa, 1991; Thomas *et al*. 1997; Poulin 1999).

Ecological investigations of these systems are often effort-intensive, yet still may not provide explanations for the phenomena observed. While released cercariae can be used to assess a snail's infection status, the only sure way (external metacercarial infections excepted) is to look for parasite stages in host tissues. An assessment of the trematodes present in a host population therefore often requires many dissections. Popiel (as cited by Irwin, 1983) must hold the record for the largest number. Over 250000 *Littorina saxatilis* from the Welsh coast were examined and only 1 was infected with *Cercaria littorinae saxatilis* V. In Ireland, Irwin (1983) found this cercaria in 31 of 350 (9%) snails (including in 7 double-species infections). This illustrates the degree of spatial heterogeneity in prevalence and variety of infections often involved in marine snail–trematode systems. There is seldom a tested, valid explanation for such differences.

My own work has been almost exclusively on the *Ilyanassa obsoleta* – trematode system in Delaware estuaries and I therefore tend to view mollusc–trematode dynamics through this eastern North American system. Commonalities among scientific phenomena are prized. It would be simpler, for example, if we could assume that the ecological determinants of freshwater and marine mollusc–trematode assemblages were the same, or that long-lived and short-lived snails are the same as resources for trematodes. System similarities are important to our understanding, but differences matter too. A comparative approach stands to inform our perspective on what drives the ecological phenomena associated with marine snails and trematodes. I will first rather extensively summarize what is known about *I. obsoleta* and its trematodes. Information is widely scattered in a literature spanning a century and a current summary of knowledge about this frequently trematode-infected and much-studied snail is warranted. Two other well-studied marine systems, those of the snails *Cerithidea californica* and *Littorina littorea*, will then be more briefly summarized and a comparison made.

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* Correspondence address: Dr Lawrence A. Curtis, Cape Henlopen Laboratory, College of Marine Studies, University of Delaware, Lewes, DE 19958 U.S.A.
E-mail: lcurtis@udel.edu

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THE *ILYANASSA OBSOLETA* SYSTEM

In a review of snails and trematodes, Esch & Fernandez (1994) wrote 'that knowledge of the biology of both the host and the parasite is imperative in order to understand the ecology of either organism.' The current comprehension of the *I. obsoleta*–trematode system is the product of such an integration. Considerable knowledge of the biology of this snail exists. Of particular note in the present context is the possession of a crystalline style (Jenner, 1956). This is a rare structure in neogastropods (Yonge, 1930) and probably accounts for *I. obsoleta's* abundance, which can be over 1000 m^{-2}. It allows the dietary utilization of an abundant food source, plant materials (Curtis & Hurd, 1979, 1981; Brenchley, 1987). Though snails consume carrion, most of the dietary intake comes from algal sources (Wetzel, 1977). The main habitats for *I. obsoleta* are mudflats, sandflats and saltmarshes on the Atlantic coast of North America. Growth and age structure were first studied in a Woods Hole population by Scheltema (1964). Egg cases are produced in the spring, from which veliger larvae emerge. After a tenure of weeks in the plankton they settle as juveniles at ~1 mm shell height. By the third summer, snails reach ~14 mm and the age of first reproduction. Growth slows after summer 3 and with yearly recruitment a local population will contain 3 size-classes, first and second summer snails plus a composite group (⩾ 18 mm) containing older individuals. Planktonic larval dispersal results in genetically homogeneous populations along the eastern seaboard of North America (Gooch, Smith & Knupp, 1972).

Miller & Northup (1926) provide early descriptions of many of the trematodes found in this snail around Woods Hole, Massachusetts. Further descriptions and elucidations of life cycles are given by later authors (Table 1). McDermott (1951) describes and figures the trematodes of *I. obsoleta* in New Jersey. Stunkard (1983*a*) lists the infecting species around Woods Hole as well as other hosts in the life cycles.

Physiological interactions of *I. obsoleta* and its trematodes are complex. They are important to consider, as they could dictate parasite transmission dynamics and changes in host growth, host or parasite survival, and spatial distribution of infected hosts. The physiological response to temperature of snails was found to be altered when infected (Vernberg, 1969; Vernberg & Vernberg, 1974). In the laboratory at 37 °C, uninfected and infected hosts survived about equally well, but at 39 and 41 °C survival of infected snails was reduced. The inference was that infection could jeopardize host survival in the intertidal zone. Riel (1975) found contrasting results wherein infected snails survived high temperatures better. Later work (Barber & Caira, 1995; Curtis, Kinley & Tanner, 2000) showed that infected snails survive in the field for years. The upper temperature tolerance of parasite stages in snail hosts was deemed an adaptation to the definitive host environment (Vernberg & Vernberg, 1974). For example, the larvae of *Himasthla quissetensis*, a bird parasite, could survive 41 °C, whereas the larvae of *Zoogonus rubellus*, a fish parasite, were killed at 36 °C. Cercariae were better able to handle salinity extremes than the snail host (Vernberg, 1969). For example, *H. quissetensis* cercariae had about the same respiratory rate from 10 to 35, while the snail's rate declined below 15 psu (= g/kg). Kasschau (1975) found no difference in reaction to salinity between uninfected and infected hosts. Adult trematodes could tolerate anaerobic conditions for a day or more, but cercariae for no more than a few hours. This could negatively affect host-to-host transmission in the sometimes reduced O_2 conditions of saltmarshes (Vernberg & Vernberg, 1974). Sindermann, Rosenfield & Strom (1957) and Sindermann (1960) showed that *Austrobilharzia variglandis* cercarial output was reduced by withholding food from hosts, salinity extremes, low temperatures, and reduced oxygen tension. The question of gigantism, i.e. enhanced growth of parasitized *I. obsoleta*, which would affect host size-infection prevalence relationships, was examined in the laboratory by Cheng *et al.* (1983). They found that enhanced growth due to infection did not occur. Neither does gigantism occur in the wild; rates of shell height change in infected individuals were much reduced (Curtis, 1995). Infected *I. obsoleta* are sterile. Among thousands of dissections of infected snails, only 2 individuals still had gametes (Curtis, 1997). Cheng, Sullivan & Harris (1973) and Pearson & Cheng (1985) showed that castration by *Z. rubellus* infections results from a parasite secretion.

Trematodes affect snail movement and spatial distribution. There is a tendency for *I. obsoleta* to move to subtidal areas as winter approaches (Batchelder, 1915), but Sindermann (1960) noted that this was inhibited by infecting *A. variglandis*, *H. quissetensis* and *Z. rubellus*. Emphasizing the effects of *A. variglandis*, the following sequence was reported. In spring, snails move to the upper shore where migratory birds (the source of snail infections) congregate. Snails gain infections and infected snails shed cercariae, which infect bird hosts. Snails remain in the higher intertidal zone in summer and prevalence there increases to ~25%. In autumn, uninfected snails move into subtidal winter aggregations, but infected snails tend to remain on the upper shore. The snail population overwinters essentially in this state. Partly to assess the findings of Sindermann (1960), Stambaugh & McDermott (1969) studied the effect of trematode infections on locomotion of *I. obsoleta*. In the laboratory, they studied 6 species of trematodes, but mainly *A.*

Table 1. The trematodes of the estuarine snail *Ilyanassa obsoleta* encountered in Delaware, USA and other hosts in the life cycles

Trematode	Cercariae produced in	2nd host (example)	Definitive host	Reference(s)
Himasthla quissetensis	rediae	bivalve	bird	Stunkard (1938*a*)
Lepocreadium setiferoides	rediae	flatworm	fish	Martin (1938); Stunkard (1972)
Zoogonus rubellus	sporocysts	polychaete	fish	Stunkard (1938*b*)
Austrobilharzia variglandis	sporocysts	none	bird	Stunkard & Hinchliffe (1952)
Gynaecotyla adunca	sporocysts	crustacean	bird, fish	Rankin (1940); Hunter (1952)
Stephanostomum dentatum	rediae	fish	fish	Stunkard (1961)
Stephanostomum tenue	rediae	fish	fish	Martin (1939)
Diplostomum nassa	sporocysts	unknown	unknown	Martin (1945); Stunkard (1973)
Pleurogonius malaclemys	rediae	*I. obsoleta*	terrapin	Hunter (1961; 1967)

variglandis, *H. quissetensis*, and *Z. rubellus*. There was much individual variation in locomotion, but Sindermann's results were supported, as tendency to move and rate of locomotion were reduced in infected snails. In Delaware, *A. variglandis* is infrequent (Curtis, 1997) and these migration patterns have not been seen. Nevertheless, the vertical position of the collection site and the particular trematodes present can greatly influence observed prevalence.

An *I. obsoleta* population on an apparently homogeneous sandflat, Cape Henlopen in Delaware Bay, was investigated by Curtis & Hurd (1983) and much unanticipated spatial heterogeneity was found. Infection prevalence increased exponentially with snail size, suggesting that snails do not lose infections. That larger snails were more likely to harbour trematodes added to infection prevalence heterogeneity because size classes were patchily distributed. Two trematode zones on the sandflat were identified, though no obvious physical feature was involved. There was much variation within zones, but in the southwest area a smaller proportion of snails was infected than in the northeast, where prevalence was generally 50–100 %. An overall analysis showed that snails $\leqslant$ 18 mm shell height were seldom infected in either zone; snails $\geqslant$ 24 mm were infected wherever found; however, for unknown reasons, snails 19–23 mm showed greater trematode prevalence in the northeast section. It was determined that samples representative of the populations of snails and/or trematodes on the sandflat would be difficult to obtain.

Certain aspects of the spatial heterogeneity were later explained. Feeding aggregations on carrion promote snail growth and survival (Curtis & Hurd, 1979) and reproduction (Hurd, 1985). Curtis (1985) investigated the roles of snail sex and parasitism in forming these aggregations. In carrion-response experiments, control samples from enclosures estimated the proportions of resident snails of each sex that were infected with different trematodes. Responding snails crawling to carrion at the upstream end of enclosures were examined. Uninfected females, in reproductive condition, responded to carrion more often than males and carrion aggregations are often largely composed of females. Parasite influence could be detected only after the breeding season; e.g. *L. setiferoides*-infected snails of both sexes responded preferentially to carrion. Thus, trematodes can affect snail distribution other than by merely inhibiting locomotion.

Another behaviour alteration affecting snail spatial distribution was discovered. Curtis (1987) found that most snails stranded above the waterline by falling tides on beaches and sandbars had *Gynaecotyla adunca* infections. To investigate this pattern, a plot on a sandbar peak was cleared of snails on an initial low tide and subsequently on 29 low tides over a 2 week period. Snails recovered in the plot following high-waters were almost always *G. adunca*-infected; more were found on night low tides, and many harboured multiple-species infections. Usually, transmission-enhancing adaptations work through predation. The next hosts of *G. adunca* are semi-terrestrial amphipod or decapod crustaceans and they must be reached by cercariae (Rankin, 1940). Since hosts are castrated when infected, and since only *G. adunca*-infected snails frequented the upper shore, it was deduced that this altered behaviour was a parasite adaptation resulting in enhanced cercarial transmission to the second intermediate host.

Curtis (1990) followed the movements of individual *G. adunca*-infected snails. Two groups of 250 snails were collected: in one group, collected in the high intertidal zone, snails were likely to be infected with *G. adunca*; snails in the other group, collected lower down, were not. Snails were individually marked, released around a sandbar peak, and their locations noted on 16 subsequent low tides. Only *G. adunca*-infected snails were frequently seen near the sandbar peak and their preference for visiting on dark low tides was confirmed. Some individuals bearing this parasite visited the sandbar repeatedly, suggesting a regular migration. Curtis

(1993) investigated when and where *G. adunca* cercariae were released by infected snails. Hosts, harbouring active cercariae, began their upward migrations mostly on afternoon flood tides. As they were later left emerged by receding tides at night, they produced mucus trails containing perhaps thousands of cercariae. Oddly, trails left on daytime ebbing tides lacked cercariae. Cercariae are thus left where probability of reaching a nocturnal, semi-terrestrial, crustacean second intermediate host is greatest. How these migrations are cued and controlled is unknown.

Recently, McCurdy, Boates & Forbes (2000) described a different spatial distribution of *G. adunca*-infected snails in the Bay of Fundy. There the prevalence of *G. adunca* was greater in snails vertically lower down, associated with the distribution of the amphipod second host in that habitat. What might explain this curious geographical and distributional difference? Possibly the parasite is universally adapted to adjust the zonation of its first host according to which second intermediate host is available. Or, there may be differently evolved parasite ecotypes.

Longevity of individuals in a population is important from many perspectives, not least the accumulation of parasites. This snail has been cited as living 3 (Hyman, 1967), 5 (Scheltema, 1964) and 7 years or more (Jenner & Jenner, 1977). Earlier estimates of longevity were based on population-level studies. Curtis (1995) followed the growth histories of individual snails (most $\geqslant 18$ mm shell height) in the field. In 1991, 1200 snails from an infrequently parasitized population that had further tested uninfected by failing to release cercariae, were individually marked, measured, and released onto Cape Henlopen. In 1993, another 200 such transplanted snails plus 300 native Henlopen snails were released. Marked snails were located and shell height changes noted through summers and autumns of both release years. Uninfected ($n = 173$) and infected ($n = 49$) snails were recovered. For uninfected snails, those initially smaller grew a little faster than those initially larger. Mean growth was 1·2 mm y^{-1} with considerable variation (95% confidence interval ±1 mm). Growth of infected snails was much slower, estimated at 0·2 mm y^{-1}. Snails are longer lived than previously thought. A 27 mm snail, infected or not, was estimated to be 30–40 years old. Further, in the area where this study was done 98% of 23 mm snails were already infected (Curtis & Hurd, 1983). Since many $\geqslant 25$ mm infected snails were observed, which would require at least an additional decade of growth, it was inferred that infections persist for at least 10 years. Thus, hosts and infections live long and the *I. obsoleta*–trematode system is slowly paced.

A study done in the Savages Ditch area of Rehoboth Bay, Delaware, where many infected individuals occurred, confirmed this (Curtis *et al.* 2000). On Cape Henlopen 27 mm snails are scarce, while some Savages Ditch snails reach 37–39 mm. Is this the result of locally faster growth or greater age? Transplanted snails ($n = 249$), which had tested as uninfected, and native snails ($n = 231$), which were mostly already infected, were marked and released in 1996. Growth of uninfected snails was about the same as on Cape Henlopen (mean = 1·5 mm $y^{-1} \pm 0{\cdot}7$, $n = 86$). Some infected snails provided 4 year-long field growth histories. Growth rate, based on 94 infected snails, was again estimated at $\sim$ 0·2 mm y^{-1}. Probable size at infection, the large size attained, growth rates, and habitat history, suggested that some snails stood to be as old as 60–70 years.

The long lifespan of the host must be coupled with the slow rate at which trematodes colonize snails. The 1991 and 1993 releases (above), totaling 1400 putatively uninfected snails (sentinels), assessed the probability of a snail becoming infected while in the field. These sentinels were released into an area where trematode prevalence was high (80–90%) and it was expected that sentinels would quickly become infected. However, 185 sentinels were recovered after being free a mean of 87 d (range = 17–793) and only 1·6% carried new infections (Curtis, 1996). The 249 sentinels released in 1996 at Savages Ditch, another high prevalence site, mostly disappeared from the release area and only 16 were recovered after being free for 104–776 days. Two became infected (over 2 years) and the infection probability estimate was 6·3% y^{-1} (Curtis & Tanner, 1999). Juveniles are uninfected at settlement and support for a low colonization rate can be gained from the low infection prevalence in snails 1–2 (1·2%) and 3–4 years old (4·0%) (Curtis, 1997).

Curtis & Tanner (1999) also considered native snails from both Cape Henlopen and Savages Ditch that had certain infections when released. These served to gauge the probability of changes in infecting species composition over time. Apparent changes, however, must be interpreted wisely because if snails fail to release cercariae of all species harboured when tested, which happens (Curtis & Hubbard, 1990), infections will be incorrectly assessed. Most hosts demonstrated the same infecting species for their whole time free [currently up to 6 summers at Savages Ditch (Curtis, unpublished data)]. In total, 6 of 123 (4·9%) native snails recovered over multiple years had clearly changed infecting species composition. The probability of a host changing infection status is therefore low, clearly under 5% y^{-1}. Thus, a snail might easily go a decade and more without adding or losing infecting species. Host and infection longevity, not rapid colonization, are the keys to accumulation of single and multiple infections in populations.

Assemblages of trematode species infecting individual snails (infracommunities) were recently reviewed by Esch, Curtis & Barger (2001). DeCoursey & Vernberg (1974) first studied these assemblages in *I. obsoleta*. They had only a few multiply-infected snails to work with, but determined that in double infections, there was some displacement of stages from the usual sites occupied in single infections. They also counted *L. setiferoides* and *Z. rubellus* cercariae produced in a 24 h period by singly- (n = 5 and 3, respectively) and doubly-infected (n = 2) snails. The double infections produced fewer cercariae.

Curtis (1985, 1987, 1990) noted that multiple infections are relatively common in *I. obsoleta*, particularly if infected by *G. adunca*. Curtis & Hubbard (1993) took advantage of this to collect snails harbouring a variety of multiple infections from a sandbar where *G. adunca* was common. They collected 18 uninfected snails, 162 with single infections (5 species), 134 with double infections (11 combinations), and 65 with triple infections (5 combinations). Using these snails, they considered 4 possible evolutionary models for trematodes using this host: (1) parasites are adapted to the host; (2) the host is adapted to the parasites; (3) parasites are adapted to the host and to each other; and (4) there is a combination of (2) and (3), where all players are adapted to each other. With regard to (1), it was taken for granted that the trematodes are adapted to this obligatory host since they must encounter it in each life cycle. Number (2) would require that hosts encounter trematodes in succeeding generations. If so, hosts might be able to resist infection by the common species. Number (3) would require that succeeding generations of trematodes co-occur in infracommunities. Adaptations might be expected such that one species could counter (or possibly facilitate) co-occurrence with another species.

With regard to (2), the ability of the host to resist infections was not tested, but trematode prevalence is variable within and among *I. obsoleta* populations (Curtis & Hurd, 1983; Curtis, 1997) and the host life cycle includes an unpredictably dispersed planktonic larva. A lineage of snails bearing a mutation that, for example, defended against a particular trematode, or even trematodes in general, would not necessarily encounter the required selective agent. There is too much opportunity to exist free of trematodes. Thus, selective pressures would probably not be pervasive and consistent enough to generate host adaptations specific to trematodes. With regard to (3), adaptive relationships between trematode species, Curtis & Hubbard (1993) tested for changes in spatial distribution of trematodes within snails, and for complete suppression or reduction of cercarial output when species co-occurred. If adaptations had developed, they stood to be manifested in one or more of these ways. Much variability was encountered, but no consistent displacements of trematode larvae within snails due to co-occurrence were detected. Mostly, parasite stages occurred throughout snails in all species combinations tested. No species' production of cercariae was suppressed, nor was it significantly reduced, by co-occurrence with other species. Trematode species seemed uninfluenced by other species present in the same host. Further, in the global *I. obsoleta* population, species of trematodes only seldom and irregularly co-occur (Curtis, 1997). Definitive hosts disperse eggs of trematodes unpredictably and they may easily disperse them to sites where, even if miracidia successfully colonize a snail, the selective force (another trematode) is likely rare or absent. Therefore, the only likely adaptive relationship in this system is parasite to host.

Studies of trematode species present in *I. obsoleta* populations (component communities) usually reveal low prevalence and few multiple-species infections (reviewed in Curtis, 1997). Given problems associated with obtaining representative samples, different methods of collection and analysis, as well as actually varying assemblages across landscapes (Esch *et al*. 2001), variable results may be expected. Major works on *I. obsoleta* include Gambino (1959), who examined snails from a Rhode Island population by dissection, Vernberg, Vernberg & Beckerdite (1969), who examined snails from North Carolina, first by cercarial release and then dissection of those shedding, and McDaniel & Coggins (1972), who assessed snails from North Carolina by cercarial release. Curtis (1997) presented data from 11 774 dissections of snails from 9 Delaware sites collected between 1981 and 1995. Samples were not usually meant to be representative of the populations sampled, and because of this calculations were not made to compare observed and expected frequencies of multiple infections, as is sometimes done (e.g. Vernberg *et al*. 1969). Results would probably have given some erroneous impressions. Overall, 51·04 % of snails were infected (range across 9 sites = 8·7–100 %) with 1 or more species. Five core species (occurring in $\geqslant 1\,\%$ of snails) and 4 satellite species (occurring in $< 1\,\%$) were noted. Of snails examined, 12·57 % carried multiple-species infections, usually involving core species. There were 16 double, 7 triple, and 1 quadruple combinations. This large *I. obsoleta* sample, admittedly biased toward older snails and a high prevalence site (Cape Henlopen), had greater prevalence of single and multiple infections than any so far collected. Gambino's (1959) sample was most similar; 25·66 % of 5717 snails were infected and 0·91 % had unspecified double infections.

SYSTEMS FOR COMPARISON

Cerithidea californica and its trematodes bear comparison with the *I. obsoleta* system. The natural history of this snail, which occurs from just north of

San Francisco to central Baha California, is treated by Race (1981). This intertidal saltmarsh inhabitant is a mesogastropod (herbivorous) deposit feeder. It sometimes reaches densities of $> 1000\,\text{m}^{-2}$. Juveniles crawl away from the egg case and adults are mostly sedentary, leading to limited gene flow among populations. Young snails are about 0·25 mm at release in June, reach 3 mm by August, cease growing in winter, and by the end of the second summer are ~ 15 mm. Size at first reproduction is ~ 20–24 mm, probably when 3 years old. The specific habitat occupied and snail size can affect growth rates. Growth of snails in submerged pans is faster (~ 4 mm mo^{-1} for 15–20 mm snails) than those in emerged pans or on mudflats (~ 1 mm mo^{-1}). Snails 20–25 mm grow only about 1 mm mo^{-1} and snails >25 mm slower still. Individuals >30 mm are often observed and a longevity of 8–10 years is given by Sousa (1983), 20 years by Byers & Goldwasser (2001).

Populations of this species can have substantial trematode prevalence, but there is much spatial variability (Lafferty, 1993*a*). Birds are the definitive hosts of all trematodes in this snail (Sousa, 1983). Martin (1955) examined 12 995 snails $\geqslant$ 20 mm, that were collected over a year at a bird congregation site in Upper Newport Bay, California. Overall, trematode prevalence was 66·79 % and double (38 combinations) and triple (9 combinations) infections occurred in 5·31 %. At other California sites prevalence was lower and multiple infections fewer: in Gloleta Slough prevalence was 15·4 % (n = 2910), with 0·45 % doubles (5 combinations) (Yoshino, 1975); in Bolinas Lagoon overall prevalence was 16·90 % (n = 25 859, over 7 years) and 0·35 % had multiple infections (21 double combinations plus a single occurrence of a triple) (Sousa, 1990).

Trematode-induced behaviour alterations affecting aggregation and movement of *C. californica* have not been reported. Sousa (1983) noted that infected snails did not exhibit copulatory behaviour. Growth of infected snails is stunted (Sousa, 1983; Lafferty, 1993*b*). Sousa (1983) illustrates increasing prevalence with size, all snails $\geqslant$ 33 mm being infected. Infections appear to be permanent and greater prevalence in older snails might be predicted because they have been longer exposed to infection. At sites regularly visited by definitive hosts, high trematode prevalence can occur, e.g. Martin's (1955) collection site. Data seem not to exist on the probability that an uninfected *C. californica* will become infected. However, Sousa (1993) reports that, of 1170 snails previously infected, 8·3 % changed infections during field release times up to 4·1 years. This shows that infected snails can live for years. It also suggests a low colonization rate, as does the few infections in 1–2 years old snails (Sousa, 1983).

Littorina littorea and its trematodes may also be compared with the *I. obsoleta* system. This abundant mesogastropod is native to European waters, but occurs in eastern North America and on the Pacific coast as well (Carlton, 1969). Larvae are planktonic, gene flow is substantial, and populations are genetically homogeneous over broad regions (Berger, 1977). Distribution on shores is variable. Around England and the North Sea coast of Germany it occurs mostly on rocky intertidal shores. In the Baltic Sea, with its reduced salinity and tidal range, its vertical distribution is displaced downward into the subtidal zone (Lauckner, 1984). On a Wadden Sea tidal flat, Saier (2000) found that all but a few large adults occur intertidally and recruitment occurs there. In North America, this snail was first reported in Nova Scotia in 1840 and has subsequently spread southward (Berger, 1977). It displaces co-occurring *I. obsoleta* (Brenchley & Carlton, 1983). In Nova Scotia, juveniles recruit subtidally and then move shoreward (Lambert & Farley, 1968). A migration from the high to low intertidal zone occurs in autumn, but this is not seen in Europe (Sindermann & Farrin, 1962; Lambert & Farley, 1968).

On age and growth of *L. littorea*, Moore (1966) notes that sexual maturity is attained when 2 or 3 years old. Hyman (1967) gives a longevity of 4–10 years, 20 years in captivity, with snails reaching ~ 27 mm shell height in 4·5 years. Hughes & Answer (1982) indicate that snails attain ~ 12–15 mm in 1 year, ~ 18–20 mm by 2 years, and with subsequently slower growth they reach an asymptotic size at 30 mm. Robson & Williams (1971) note that some reach larger than 30 mm. In Nova Scotia, growth rates are similar and the largest snails are $\geqslant$ 4 years old (Lambert & Farley, 1968).

The extensive data on prevalence and diversity of trematode infections in *L. littorea* show variability within and among regions (Table 2). In England, James (1971) lists 11 trematode species; on North Sea coasts, Lauckner (1980) lists 6. *Podocotyle atomon* uses a fish definitive host, but all other species use birds and 4 of these occur in Baltic Sea *L. littorea* (Lauckner, 1984). In North America, trematode diversity in this snail is lower. Stunkard (1983) lists 2 species and Pohley (1976) 3, one observed only once. An important trematode, common to both sides of the Atlantic and the Baltic Sea, is *Cryptocotyle lingua*. Double infections are most common on the North Sea coast of Germany (Werding, 1969; Lauckner, 1980), where 7 different combinations are recorded (Table 2). Triple infections are not reported in *L. littorea*.

Effects on migratory behaviour can be pronounced. In Maine (Sindermann & Farrin, 1962) and Nova Scotia (Lambert & Farley, 1968) the down-shore movement of snails for winter is inhibited by infections with *C. lingua*. Williams & Ellis (1975) followed the vertical movements of marked uninfected and infected snails for 8 weeks in Yorkshire, England. Uninfected snails moved down-

Table 2. Trematode prevalence observed in *Littorina littorea* populations. Number of species combinations is given in parentheses

Locality	Number of snails examined	% infected	Number of trematode species	% doubles	Reference
West England	2500	3–4	7	—	Rees (1936)
West England	6165	4·8	6	—	James (1968)
West England					Hughes & Answer (1982)*
Orme area	60	31·7	?		
Porth Cwyfan	299	3·0	?		
Trwyn-Penrhyn	289	7·6	?		
Gorad-y-Gyt	230	17·0	?		
Foryd Bay	377	18·6	?		
South England (Plymouth)					Rees (1936)
Drake Island	220	10·0	2	—	
Trevol	550	2·0	2	—	
South England	800+	13·3	3	—	Watts (1971)
East England					Robson & Williams (1970)
Scalby Rocks	5878	39·9	4	2·5 (2)	
South Bay	1009	3·2	?	—	
Scalby Pipe	1194	20·7	?	—	
Burniston Bay	434	2·5	?	—	
East Scotland (Ythan Estuary)					Huxham *et al.* (1993)
Newburgh Quay	200	11·5	3	—	
Quay Inches	200	14·5	4	—	
Burnmouth Scalp	200	2·5	1	—	
Sheepfold Burn	200	6·0	2	—	
Northern Ireland (Belfast)					Matthews *et al.* (1985)
Portavogie shore	101	52·5	3	—	
Portavogie offshore	300	65·3	3	1·0 (2)	
German North Sea coast					Lauckner (1980)
North Sea coast	2691	42·8	6	3·3 (7)	
Isle of Sylt	30811	19·4	6	—	
Schleswig-Holstein	1496	5·7	6	—	
Baltic Sea/Kattegat	11571	15·0	5	—	
Baltic Sea/Kattegat					Lauckner (1984)
Neustadt Bay coast	471	1·6	4	—	
Neustadt Bay 16 m	577	18·7	2	—	
Sletterhage 20–26 m	334	12·6	4	—	
New England (Isles of Shoales)					Hoff (1941)
gull feeding area	501	6·2	1	—	
gull roosting area	86	19·8	1	—	
gull nesting area	134	20·9	1	—	
around docks	96	0·0	—	—	
New England (Maine)					Sindermann & Farrin (1962)
high-tide zone	3000	65·0	1	—	
mid-tide zone	3000	45·0	1	—	
low-tide zone	3000	46·0	1	—	
New England (Maine and Rhode Island)					Pohley (1976)
Eastport	464	1·5	1	—	
Rogue Bluffs	651	10·5	3	—	
Watch Hill	925	2·4	2	—	

* These authors wrote generally of 4 species of trematodes and found 2 double infections in 2 species combinations.

ward a few metres in winter; snails infected with *C. lingua* rediae or *Renicola roscovita* sporocysts moved downward less than uninfected snails. Here, similar to *I. obsoleta*, the effects on hosts of trematodes themselves can bring about spatial heterogeneity in prevalence.

Trematodes have extensive detrimental effects on *L. littorea* (Lauckner, 1980). Infection causes, if not outright castration, a severe reduction in gonadal output (Huxham, Raffaelli & Pike, 1993). Probability of bearing an infection increases with size (age) (e.g. Lauckner, 1980; Hughes & Answer, 1982). *Renicola roscovita* is found only in smaller adults, but the general notion is that only adult *L. littorea* can be infected (James, 1968; Robson & Williams, 1970; Lauckner, 1980). However, snails <1 year old can be infected. Lambert & Farley (1968) make note of a few snails <11 mm infected with *C. lingua* in Nova Scotia. In England, Robson & Williams (1970) recorded 2 species infecting <10 mm snails and 3 infecting 10·1–15·0 mm snails (sometimes doubly). Infections in immature snails do occur, but are seldom recorded, possibly because prevalence is low and such hosts are less frequently examined.

Several authors have considered enhanced growth (gigantism) in infected *L. littorea* and it seems not to occur. Robson & Williams (1971) could not confirm or deny it and Hughes & Answer (1982) found growth unchanged. Huxham *et al*. (1993) noted that growth of caged, infected snails in Scotland was very slow or stopped. Mouritsen, Gorbushin & Jensen (1999) found that, depending on habitat, growth is either stunted or unaffected.

Longevity of infections in *L. littorea* has been studied. Rothschild (1942) observed an active *C. lingua* infection in the laboratory for 7 years. This alone makes the case for potentially prolonged viability. Robson & Williams (1970) kept snails in the laboratory infected with *C. lingua* (n = 49), or *Cercaria A* (*Renicola roscovita*) (n = 35), or both (n = 3) for 6·5 months. At the end of that time, 3 initially shedding *C. lingua* and 11 *R. roscovita* had died, some (n = 4) had lost their infections, and 8 snails were unaccountably lost. All 3 double infections survived. The frequent death of *R. roscovita*-infected snails suggested that this trematode is ultimately lethal to the snail. Huxham *et al*. (1993) caged a total of 800 uninfected and infected snails in the field over 530 days, 96 died, 16 were lost, and infected snails were somewhat more likely to die. Large *L. littorea* are not heavily preyed upon by birds and mortality among them was attributed to trematodes.

There is little information on the colonization rate of *L. littorea* by trematodes, but it appears to be low. Hughes & Answer (1982) did not estimate a rate but hypothesized that the total risk of a snail becoming infected is constant throughout life, though for a particular trematode it could vary in time. As described above, immature snails can be infected and prevalence increases with size (age). In their study of snail movement, Williams & Ellis (1975) noted that none of their uninfected snails became infected during 2 months of shore exposure.

A COMPARISON

In their native areas, one feature the *I. obsoleta*, *C. californica* and *L. littorea* systems have in common is a widespread, abundant host and a diversity of infecting trematodes. That long-standing residence within a geographic region matters to trematode diversity seems clear. The native area for *C. californica* is the southern west coast of North America where 18 species infect the snail (Ching, 1991). The native area for *I. obsoleta* is the eastern seaboard of North America where at least 9 species infect it (Table 1). It has been introduced on the west coast (Race, 1981), but only 1 species, *A. variglandis*, has been reported there (Grodhaus & Keh, 1958; Ching, 1991). The native area for *L. littorea* is Europe, where up to 11 trematodes infect it (James, 1971). Berger (1977) reported fossil *L. littorea* shells from Nova Scotia estimated to be ∼ 700 years old. This suggests a resident population prior to European colonization of North America. He posits that the modern snail population passed through a genetic bottleneck from this older population. If so, it would be instructive to have an indication of trematode diversity in the ancestral population. There may have been a parasite bottleneck as well. Currently, only *C. lingua* is common (Pohley, 1976; Stunkard, 1983). In western North America, Ching (1991) lists no infecting species. In non-native areas then, because of the few available species, multiple infections do not occur in *I. obsoleta* or *L. littorea*. This historical factor largely determines the species richness and variety of infra- and component trematode communities.

The difficulty of obtaining samples that, even if taken at random, are representative of populations is an important consideration. This is analogous to the problem of unwittingly including parasitized hosts in experiments on supposedly unparasitized hosts (Curtis & Hurd, 1983; Lauckner, 1987) because much unexplainable or misinterpreted variability may result. The point in emphasizing the general spatial heterogeneity inherent in these systems, and particularly the effects of trematodes on the spatial distribution of their hosts, is that species prevalence estimates stand to be affected. Prevalence estimates may be incorrect with respect to the general conditions under which snails become colonized, if such general conditions exist. If so, predictions about probability of species co-occurrences by way of a null model, basically making predictions by multiplying trematode prevalence estimates together, will be in error.

Examples of infected snails occupying restricted portions of the general host distribution can be noted in *I. obsoleta*. Unanticipated spatial heterogeneity, involving both parasites and host, was discovered in a sandflat population (Curtis & Hurd, 1983). The basis for some of it was later explained (Curtis, 1985, 1987) but if samples had been unknowingly taken where certain trematodes are common, such as from the northeast section of the sandflat, carrion aggregations after the breeding season, or beaches and sandbars during summer, invalid interpretations might have emerged. In the global population, these are special, unrepresentative situations. The abundance of certain infections might have been considered a consequence of an influx of definitive hosts and a matter of seasonal variation. However, this host and its infections live long and seasonality has little to do with the infections found in a sample (Esch *et al*. 2001). If a sample were collected from a sandbar, where *G. adunca* (with its attendant multiple-species infections) is common, it might have been concluded that species interactions within snails are much more frequent and important than is actually the case. On the obverse of this point, as extensive as the sampling of Curtis & Hurd (1983) was, they did not even detect *G. adunca* infecting snails because they did not happen to take samples from sandbars. Had probabilities of co-occurrences been calculated, an important species in this regard would have been utterly missed. Sindermann & Farrin (1962), Lambert & Farley (1968), and Williams & Ellis (1975) signal similar concerns with *L. littorea*. This style of analysis, with the trematode species considered here and others, has often been done (e.g. Vernberg *et al*. 1969; Lauckner, 1980; Kuris & Lafferty, 1994) and species interactions are sometimes concluded to be important in structuring trematode component communities. Knowledge of both host and parasite ecology, sampling wisdom, and caution would be wisely exercised before drawing inferences.

Complex trematode assemblages do not occur everywhere snail populations do. All three hosts considered are abundant and trematode prevalence in all three can be locally high, with the consequent presence of relatively frequent multiple-species infracommunities. High prevalences are often associated with substantial input of infective propagules from definitive hosts (e.g. Hoff, 1941; Martin, 1955; Robson & Williams, 1970; Curtis, 1997). A recent field experiment with an estuarine snail, *Cerithidea scalariformis*, confirms this connection (Smith, 2001). Host longevity is another factor in common. *Ilyanassa obsoleta* longevity is extraordinary, with individuals living for several decades (Curtis, 1995; Curtis *et al*. 2000). Longevity of *C. californica* (Sousa, 1983) and *L. littorea* (Hyman, 1967) is 1 or 2 decades. Single and multiple infections also seem to live long in all 3 hosts. In *I. obsoleta*, Curtis (1995) inferred that infections persist for 10 years or more; Curtis & Tanner (1999) observed only a few infracommunity species composition changes in the field over 3 years and Curtis *et al*. (2000) observed the same snail infected with the same trematode species for up to 5 years. In *C. californica*, infections seem permanent and long-lived (Sousa, 1983). Infracommunity composition does change (Sousa, 1993), but relatively infrequently. No data on probability of *L. littorea* changing infection status in the field seem to exist, except for the lack of new infections among the marked snails of Williams & Ellis (1975). *Renicola roscovita* (Robson & Williams, 1970) apparently causes the death of this snail and, in the laboratory, individuals sometimes lose infections (Robson & Williams, 1971). In any event, overall prevalence increases with snail age (Lauckner, 1980) and most infections persist throughout the host's life. In the trematode component communities harboured by certain populations of these snails, gradual colonization of long-lived hosts by long-lived infections seems of importance in the accumulation of high prevalence and a variety of multiple infections. If colonization is disrupted naturally, or by human impact (Lafferty & Kuris, 1999), high prevalence will not develop.

If the longevity of hosts and infections is substantial, even a low colonization rate will lead to high prevalence, and a low rate seems to be the case in all three systems. This is most clear in *I. obsoleta* where direct assessments of field colonization rates exist (Curtis, 1996; Curtis & Tanner, 1999). If prevalence of single and multiple infections were to be high in cases of shorter-lived snails and infections, it would likely stem from a higher colonization rate.

With regard to interspecific adaptive relationships in these three systems, Williams' (1966) admonition is relevant: 'adaptation is a special and onerous concept that should be used only where it is really necessary.' If there are evolutionary (adaptive) relationships between species in snail–trematode systems, it is important to recognize them because these relationships and their consequences would be pervasive and ecologically important. For adaptions to develop, all conditions must be in place for natural selection to work. The view presented here is that, in the global snail or trematode populations considered, selection pressures emanating from other species can be rarely encountered and certain adaptive relations are unlikely to evolve.

In all three systems, trematodes must be adapted to use their snail hosts, as the snail environment is a necessary part of each life cycle. However, the possibility of the host being adapted to the presence of trematodes is less certain. The *C. californica* system is interesting in this regard. Because of crawl-away juveniles, gene flow is limited and local snail populations could possibly become differentially adapted to trematodes. Lafferty (1993*a*) may have identified such a situation. This snail matures at smaller sizes where trematodes are highly prevalent. In a reciprocal transplant experiment, he collected 550 immature snails from a site with 52% prevalence and 660 immature snails from a site with 0% prevalence. Snails were marked and some were released into their native environments as controls, others were transplanted either from the high to low, or low to high, prevalence sites. In essence, snails from the high prevalence site retained their smaller maturation size in both their own environment and the low prevalence environment; larger maturation size was retained by low prevalence site snails in both situations. Are these different adaptive responses of local host populations to parasite prevalence, or are all populations adapted similarly and this is a local environmentally induced response, perhaps parasite-mediated (e.g. miracidial presence signals snails to mature earlier)? The question could not be definitively resolved, but a genetic difference between populations is suggested. If local populations of this snail can evolve adaptive responses to trematodes, this would be unique among the three systems considered because both *I. obsoleta* and *L. littorea* have planktonic larvae and gene flow among populations is extensive (Gooch *et al*. 1972; Berger, 1977). If a host has a widely dispersed planktonic larva, it would be difficult or impossible to develop adaptations to trematodes because of spatial heterogeneity in trematode occurrence (Curtis & Hurd, 1983; Curtis & Hubbard, 1993; Curtis, 1997; Table 2). A veliger larva bearing a mutation that would help it resist a future trematode infection would not necessarily encounter the selective pressure at the site where it metamorphosed into a benthic juvenile. Whatever fitness benefit there might have been would seldom be gained. Until we can follow host genotype dispersal by planktonic larvae [see DiBacco & Levin (2000) for an advance in this area] and couple it with spatial heterogeneity in trematode prevalence, this argument will depend on what we do not know about planktonic larval dispersal rather than what we do.

The potential for trematode species to be adapted to one another seems remote in all three systems. Multiple infections are generally scarce and patchy in spatial distribution. A trematode genetic strain with a heritable advantage, in dealing with another trematode species on co-occurrence in a snail host, would have it eggs dispersed by a vertebrate definitive host, which may well disperse the eggs to sites where the other trematode, the supposed selective pressure, is rare or absent. On this reasoning, trematode species co-occurring in the same snail is an infrequent ecological accident. How they get along would be based on the one adaptational constant in these systems, how each species is adapted to utilize the host. So, for example, Esch *et al*. (2001) noted that rediae have a mouth and are adapted to 'chew' on host tissues. If rediae eat the stages of another trematode, which they sometimes do (e.g. Sousa, 1993), it results from the way rediae are adapted to utilize the host, not an adaptation to counter the presence of another trematode. In Williams' (1966) terms, chewing on host tissue would be a 'function' (directly selected), chewing on other parasites would be an 'effect' (not directly selected).

To support or refute the existence of adaptive relationships among species in snail-trematode systems, would require specific data on some very large-scale systems. For starters, answers to these questions would be needed: (1) how patchily are snail populations with intense trematode presence distributed? (2) what is the probability that planktonic larvae will be dispersed to these patches? and (3) what is the probability that definitive (and possibly other) hosts will disperse trematode propagules to these patches? The answer to the first seems to be that high prevalence sites are quite localized. The second and third are not answerable at present, but there must be substantial probability that veliger larvae and trematode eggs will be scattered among various host populations, many of which lack high trematode prevalence. Natural selection leading to interspecific adaptations under these circumstances is reasonably questioned.

Another factor diluting chances of larval trematodes being adapted to each other is that some trematodes can use alternate snail species. In *I. obsoleta*, taxonomic uncertainties could be involved, but *H. quissetensis* was reported in *Nassarius vibex* by Holliman (1961) and Rohde (1977) suggested that *Austrobilharzia terregalensis* is probably synonymous with *A. variglandis* and has a worldwide distribution in a variety of snail species. In *C. californica*, only *Parorchis acanthus* also occurs in other snail species (n = 2) (Ching, 1991). For trematodes in these two systems, then, there is limited latitude as to host snail selection. However, *L. littorea* co-occurs with several congeners and trematodes may infect any of several hosts. In North America, Stunkard (1983) lists the trematodes of 3 littorinid species, *L. littorea*, *L. obtusata*, and *L. saxatilis*. *Cryptocotyle lingua* occurs in all 3, as does *Cercaria parvicaudata*. In Europe, there are more parasite species and a greater diversity of littorinids. James (1971), working mainly on the coast of Wales in England, lists *L. littorea*, *L. littoralis*, *L. neritoides* and *L. saxatilis* (with 4 subspecies). In *L. littorea* 11 trematodes are listed, 6 as occurring exclusively in *L. littorea*. However, 1 of the 6 is *C. lingua*, which has been observed in other littorinids (Lauckner, 1980; Stunkard, 1983). Thus, 6 of 11 species may be listed as infecting multiple littorinid hosts. If trematodes can use alternate snail hosts, the host–parasite system becomes increasingly diffuse and likelihood of establishing adaptations between trematodes in any 1 snail host is even less.

CODA

Questions of how frequently multiple infections occur in marine snails, and how they form and persist, have been addressed recently by several authors (Lauckner, 1980; Sousa, 1990, 1993, 1994; Kuris, 1990; Kuris & Lafferty, 1994; Lafferty, Sammond & Kuris, 1994; Curtis, 1995, 1997; Esch *et al*. 2001). Often these questions have been addressed from a statistical point of view, using component community patterns to infer infracommunity dynamics. Relatively frequent multiple trematode infections have been observed in certain populations of all three snails considered here. When species co-occur in individual snails, consistent patterns of association may emerge, and these dictate to some extent the variety of multiple infections observed in component communities. Examples are:

in *I. obsoleta*, *H. quissetensis* and *L. setiferoides* seldom occur in the same snail, but these species variously co-occur with *Z. rubellus*, *G. adunca* and *A. variglandis* (Vernberg *et al*. 1969; Curtis, 1997); in *L. littorea*, *Himasthla elongata* cohabits with *R. roscovita*, but apparently never with the common *C. lingua* (Lauckner, 1980); and in *C. californica*, *Parorchis acanthus* and *Himasthla rhigedana* do not often coexist with other species, except the schistosome *Austrobilharzia* sp. (Kuris, 1990; Sousa, 1993). These biological relationships clearly exist in infracommunities, but they are infrequent in the global populations of these marine snails. The contention here is that these relationships result from trematode adaptations to the host snail, not adaptation of one parasite to another. For parasites to be adapted to one another would require interactive infracommunities, which require frequent additions (colonizations) and eliminations of species (Holmes, 1987). In these marine snails, most clearly in *I. obsoleta*, these appear to be infrequent events and infracommunities would therefore be isolationist rather than interactive.

Valuable clues about infracommunity dynamics may be gained by using co-occurrence patterns in component communities. However, single and multiple-species infections are often embedded in host snail populations in unappreciated ways, leading to difficulties in obtaining representative samples. This is a major concern. If samples are not representative, then the inferences drawn from them may mislead. Statistical concerns aside, the connection between infracommunity dynamics and component community structure is tenuous, if not absent (Esch *et al*. 2001). Esch & Fernandez (1994) note factors internal and external to the host snail that are involved in determining the structure of trematode component communities. These three marine systems, suggest that external factors involving history and the ecological characteristics of parasites and hosts are the key. Far more important than infracommunity dynamics, are (1) frequency of definitive host visitation, (2) the availability of several trematode species, even infecting at a low rate, (3) an abundant, long-lived host snail, and (4) long-lived infections.

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