

# A perspective on the ecology of trematode communities in snails

G. W. ESCH<sup>1\*</sup>, L. A. CURTIS<sup>2</sup> and M. A. BARGER<sup>1</sup>

<sup>1</sup>Department of Biology, Wake Forest University, P.O. Box 7325, Winston-Salem, NC 27109 USA

<sup>2</sup>Cape Henlopen Laboratory, College of Marine Studies, University of Delaware, Lewes, DE 19958 USA

## SUMMARY

This paper presents a perspective on the ecology of trematodes in snail hosts based on recent evidence. Because flukes use snails almost obligatorily as first intermediate hosts, we highlight the role of gastropods as keystone species for trematodes and their communities. After reviewing recent developments in the transmission of trematodes to and from snails, we discuss trematode communities within individual snails (infracommunities) and in snail populations (component communities). Results garnered using various protocols at the infracommunity level are reviewed. The few data available, all from marine systems, indicate that low colonization rates characterize infracommunities, suggesting that trematode infracommunities tend to be isolationist in character rather than interactive. The variety of trematode species present in a component community seems to be determined by spatial overlap of definitive hosts. Relative abundance of species in a component community shows little dependence on negative interspecific interactions at the level of the infracommunity. Temporal aspects of trematode communities are related to the life history of the host snail. The component communities of long-lived snails (mostly marine) integrate many infection episodes whereas shorter-lived snails (mostly freshwater) acquire new component communities each time host cohorts turnover.

Key words: Infracommunity, component community, competition, heterogeneity, trematode, gastropod.

## INTRODUCTION

### *Snails and trematodes as keystone taxa*

The concept of a keystone species was introduced by Paine (1966). The idea is a relatively simple one. It was used to describe a species whose influence on community structure is so significant that, should the species be eliminated, the structure of the new community would be altered to such an extent it would not resemble that of the original community. In a coevolutionary context, there are no parasites which are so inextricably linked to a single group of hosts as digenetic trematodes are to snails and other molluscs. With the exception of a few marine sanguinicolids that use annelids, a mollusc is the required first intermediate host for all flukes. In this sense then, molluscs can be considered as keystone species for digenetic trematodes. The keystone concept also may be applied to many trematodes in their roles as indicator species. In the life cycles of many digeneans, an obligate, but usually passive, involvement in various predator-prey relationships at different trophic levels is a clear testimonial for many of the important food-web interactions that occur in both aquatic and terrestrial ecosystems. Accordingly, the present paper will attempt to employ, where possible, the keystone species concept as leverage in dealing with different aspects of the ecology of trematode-snail interactions.

We will begin this paper with a treatment of the basic model for trematode life cycles. Following this

brief introduction there will be three major focuses. The first will deal with transmission of eggs or miracidia to the snail host and then from the snail to another host. The latter step involves release of cercariae from the snail, which frequently may include precise patterns in the temporal emergence of cercariae. This segment in the parasite's life cycle also may embrace changes in the behaviour of the snail induced by the trematode's intramolluscan stages to ensure spatial and temporal overlap of the parasite and its next host. With many species, cercariae exhibit well-orchestrated, and always fascinating, swimming behaviour, frequently in response to physical or chemical stimuli emanating from the next host. The second major focus will deal with the establishment and maintenance of trematode infracommunities in snail hosts. Most ecologists working in this arena agree that trematode infracommunities can be either interactive or isolationist in character. Some of these investigators have argued that competition, or predation, or both, may be important factors in defining the nature of interactive infracommunities. As will be emphasized, however, the extent to which these structuring forces actually operate is under considerable discussion, and even debate. Finally, the establishment and organization of trematode component communities will be examined. At this level, especially, scale becomes an over-riding determinant. For example, spatial factors may affect success in transmission, and thereby act as a determining element in the establishment of component communities. We also will examine space within the context of landscape

\* Corresponding author.

ecology/epidemiology, a rather old concept, but one that has seen a deserved revival in recent years. Time is another major determinant of component community dynamics and it too can be related to landscape epidemiology in both ecological and evolutionary terms.

#### *Basic life-cycle patterns for snail-trematode systems*

Trematode life cycles usually require two, three, or four hosts for successful completion. There are, however, a few bizarre exceptions that do not follow these patterns. For example, Barker & Cribb (1993) reported that *Mesostephanus haliastuiris*, a prohemistomid fluke, is able to produce daughter sporocysts, cercariae, and miracidia, within mother sporocysts, suggesting the possibility of a one-host life cycle. Barger & Esch (2000) reported an opacoelid trematode *Plagioporus sinitsini*, which gives rise to sporocysts in which cercariae, metacercariae, and egg-producing adults may all occur simultaneously. They also provided convincing field evidence indicating an operational one-host life cycle for this parasite. Despite these uncommon deviations, most authorities (for reviews, see Brooks & McClennan, 1993; Poulin, 1998) agree that the three-host cycle is ancestral for digenetic trematodes, with one-, two-, and four-host cycles all being derived. Whatever the number of hosts required in the completion for any of the 25000 described species of digeneans, a mollusc must serve as the first host in the life cycle, hence the keystone character of molluscs for these parasites (a few marine sanguicolids that use annelids are exceptions to this rule).

Assuming the trematodes reach the final site of infection in an appropriate definitive host and that successful copulation has occurred, egg production will ensue. Eggs of many digeneans hatch and ciliated, free-swimming miracidia will emerge. Evidence suggests that the swimming behaviour of miracidia initially is random; at some point, however, it will be influenced by chemical agents released from the snail. After seeking out and penetrating the host, the parasite migrates internally to a final site of infection. In some species, the eggs do not hatch but must be consumed by the snail directly.

Within the snail host, the larva transforms into a sporocyst. The primary function of this larval form is to serve as a brood chamber for the next stage, or stages, in the parasite's life cycle. Normally, sporocysts remain fixed at specific internal sites, i.e. the hepatopancreas, gonads, mantle, etc., and produce either daughter sporocysts or rediae. Rediae are morphologically distinct from sporocysts in possessing a mouth and a primitive gut. The presence of a mouth permits the redia to consume host tissue directly.

All intramolluscan embryogenesis is asexual, via a process known as polyembryony. It should be noted

that whatever sequential pattern of internal development is followed, it is species specific. It should also be emphasized that all of the asexual development within the molluscan intermediate host represents, in simplest terms, an amplification of the parasite's gene pool. Whereas an adult, a miracidium, and a cercaria of the same species are highly distinct morphologically, they are nonetheless 'vehicles of the same genetic information' (Poulin, 1998).

Some species begin production of cercariae within sporocysts, others within redia. It is from this point in intramolluscan development that one can begin to see the enormous diversity in life-cycle patterns and variation in cercariae emergence and behaviour. It is this diversity and variation that then leads to ecological division among digenetic trematodes. Generally, a cercaria that emerges from the molluscan host possesses a tail and is, therefore, capable of swimming. There are many species-specific variations in the pattern of cercariae production and release, and also numerous exceptions to the swimming 'rule'. Most of the exceptions are related to the absence of a tail and, in turn, these are manifested in many ecological tendencies of trematodes.

Transmission from the snail to the definitive host usually requires a second intermediate host and, afterwards, predator/prey interaction. However, in some species, the second intermediate host is bypassed and the parasite either encysts in the open as a metacercaria or penetrates a definitive host directly. If the parasites encyst in the open, they will be accidentally ingested by the definitive host, usually a grazing mammal of some sort. Direct penetration of a definitive host by cercariae may require special behavioural coordination between the snail, or cercaria, and the definitive host. Trematode life cycles are completed when the parasites, by whatever means, gain access to their appropriate definitive hosts, and maturation and sexual reproduction can take place.

#### TRANSMISSION

##### *To the snail*

*Behaviour.* The transmission process from the definitive host to a snail invariably involves either a miracidium or an egg. When an egg is released from its definitive host, it may or may not be fully embryonated. If embryonation is required, it will require appropriate environmental conditions (e.g. temperature, light, etc.). In some species (e.g. the schistosomes) hatching of an embryonated egg is prevented until external conditions are favourable for successful transmission. Eggs of *S. mansoni*, for example, are completely inhibited by NaCl concentrations of 0.6%, but hatch readily when NaCl

concentration drops below 0.1%. This osmotic effect prevents premature hatching in the blood stream of the host.

Wright (1959) described host finding by miracidia as a 3-step process. After emerging from the egg, light or gravity, or both, stimulate the miracidium to move into a habitat most likely to be occupied by the snail intermediate host; random swimming then follows. Once positioned properly, miracidia respond to specific chemical stimuli, usually short-chain fatty acids, amino acids, or simple sugars, released by the snail host. Since the miracidium does not feed while it is free swimming, its life span is brief, generally lasting 24–36 hours. Assuming that a miracidium has responded to the appropriate stimulus, it must then locate the snail host, to which it must attach and penetrate (a comprehensive review of these processes is given by Sukhdeo & Mettrick, 1987).

Despite the simple elegance of these host-finding behaviours, the constraints involved in transmission via free-living miracidia are extensive. Species specificity by digeneans for their snail hosts and size preferences within a snail population further restrict successful transmission. Considering all of the potential risks, one might conclude that success in this phase of transmission would not be very high. In natural settings, there is a remarkable consistency in prevalences, usually ranging from 5–10%, with rare peaks as high 60% for a few species (Fernandez & Esch, 1991a; Snyder & Esch, 1993; Esch & Fernandez, 1994). Despite what may seem to be relatively low prevalences, the high capacities of intramolluscan reproduction by digeneans compensate nicely.

*Time and space.* With free-swimming larval stages, there is an obvious extension of the parasite's spatial range. As has been noted, however, eggs of many digeneans do not hatch and must instead be ingested by the snail. In these cases, there is usually extended survivorship of the parasite's eggs, providing a sort of tactical compensation in overall transmission as compared with species using free-living larval stages. Time thereby provides another dimension, in addition to space, to the transmission process (Poulin, 1998).

Whereas temporal and spatial dissemination of miracidia and eggs within a microhabitat are important in the transmission of trematodes to their molluscan hosts, the wider dispersal of digenean eggs is significant in terms of extending the parasites' geographic ranges. This is especially true for digeneans in avian hosts or marine fishes and mammals that move long distances annually. Since most of these migrations are highly seasonal, synchronization in the timing of host and parasite reproductive cycles becomes a cardinal element in the successful transmission of many digeneans.

### *From the snail*

In an excellent and very thorough review Haas (1994) relates that 'physiological analyses of cercarial behaviour have demonstrated great diversity in behaviour related to host-finding and host-recognition, even in species infecting the same host genera, and this may reflect diverse adaptations for a high success of transmission'. In another excellent review of cercaria behaviour, Combes *et al.* (1994) divided adaptations for increasing transmission probability into two categories, one of which describes the activity of parasites in terms of 'host-time' and the other in terms of 'host-space'. Here, we add another that we feel is integral to overall life-cycle success, the actual movement of cercariae to the host once 'host space' is located by the cercaria.

*Host time.* For many digenean species, the temporal emergence of cercariae from a snail is not random. Rather, it is timed very precisely, almost always being dependent on photoperiod and usually synchronized with the chronobiological behaviour of the next host in the parasite's life cycle (Combes *et al.* 1994). Several classic examples include species of *Schistosoma* that infect a range of mammalian definitive hosts in Africa. All but one of these schistosomes have a single, distinctive shedding peak during what Combes *et al.* (1994) refers to as a nycthemere, or 24 h photocycle. *Schistosoma margrebowiei*, yet another African species, has an ultradian rhythm, with two emergence peaks, one at dawn and again at dusk (Raymond & Probert, 1991). Apparently, the adaptive significance of these shedding patterns is to enhance transmission of the parasite by concentrating the short-lived cercariae within a relatively brief period of time when opportunities for contact with their appropriate definitive hosts are greatest.

*Host space.* Most mobile cercariae favourably position themselves for transmission by active swimming. This mobility can be attributed to the presence of a tail that is highly variable morphologically. The cercaria tail possesses limited glycogen stores that account, in part, for the brief transmission opportunity at this stage in the parasite's life cycle. Swimming is generally intermittent, with brief, but very intense, periods of 'tail whipping' that may either push, or pull, the cercaria, depending on the species. These flashes of activity are then followed by longer periods of drifting or sinking in the water column. A few species with reduced tail size appear to creep, in 'inch worm' fashion, on the substratum where they are most apt to encounter their benthic-dwelling crustacean hosts.

The capacity to locate within an appropriate 'host space' assumes the ability of cercariae to perceive and respond to certain types of physical provo-

cations. For most cercariae, these include light, gravity and mechanical stimuli. In the case of light and gravity, both positive and negative responses are known to occur. Whatever the nature of the stimulus, the adaptive response value rests in placing the cercariae in a position where contact with the next host in the cycle is most likely to occur. If the host is a benthic-dwelling microcrustacean, for example, then this would require a negative phototaxis or positive geotaxis, or both, on the part of the cercaria. The reverse would be called for in the case of hosts living 'up' in the water column.

Once the parasite is in the vicinity of the next host, it must respond to specific signals emanating from that host or, according to Combes *et al.* (1994), it must signal the host and cause it to respond in some favourable manner. Stimuli from the host are either of a physical or a chemical nature. In the case of physical stimuli, for example, cercariae are known to respond to water currents such as those created by movement of a fish's fin or the opercular covering the gills. Chemical stimuli are apparently rare, although cercariae of *Echinostoma revolutum* are known to respond (Fried & King, 1989) to a diasytate of *Biomphalaria glabrata*. Cercariae of *Cotylurus flabelliformis* not only respond chemically to their snail hosts, they are able to distinguish between those snails which are infected and those which are not, suggesting an ability to deter high infection intensity which might kill hosts (Fried & King, 1989).

One of the more remarkable behavioural traits to enhance parasite transmission is shown by cercariae of certain azygiid trematodes, most of which are species of *Proterometra* (see LaBeau & Peters, 1995). These furcocercous cercaria are unique in terms of their size, some with tails ranging between four and five mm in length. Also unusual is their swimming behaviour that is strikingly similar to that exhibited by larval mosquitoes. The tail furcae flap up and down, pulling the large cercariae upwards in the water column; when the flapping stops, the large cercariae settle downwards in the water column. The movement up and down is highly suggestive of a mosquito 'wiggler' and continues until the cercaria exhausts the supply of glycogen stored in the tail or the parasite is consumed by an unsuspecting, piscine definitive host. The enormous size of the cercaria apparently precludes the production of large numbers of free-swimming larvae, but the attractive behaviour compensates enough to ensure a high degree of success in transmission (LaBeau & Peters, 1995). Another adaptive quality contributing to successful transmission of these azygiids is progenesis. The body of the parasite, which is embedded in the tail of the cercaria, is usually in full egg production when it is released from the snail and almost always by the time the mime of the cercariae has attracted an unsuspecting piscine definitive host.

## THE INFRACOMMUNITY

### Introduction

In the context of the infracommunity, it is an individual of the host species that is the keystone. A number of methods have been used to study snail-trematode infracommunities. These include dissections of hosts, examination of site displacement, experimental infections, measurement of cercarial output and tracking of changes in species composition over time. Here we discuss these protocols using Wright's (1973) book as a starting point and covering important work since about the 1960s. More recent reviews of within-snail processes include those of Lie (1973), Combes (1982), Sousa (1992) and Esch & Fernandez (1994).

Wright (1973) wrote of a 'pecking order' among species coinfecting the same snail and captured the essence of much subsequent thought with his Plate XII 3, which shows an echinostome redia consuming a schistosome cercaria. He was citing work later reviewed by Lim & Heyneman (1972). This review has influenced workers on infracommunities of trematodes in snails since and must be mentioned first. Lie, Basch & Umathevy (1965) experimentally infected the freshwater pulmonate *Lymnaea rubiginosa* with various combinations of 2 echinostomes, a xiphidiocercaria, a schistosome and a strigeid. Echinostome rediae caused the demise of sporocyst infections of other trematodes, even those already established. Subsequently, Lim & Heyneman (1972) developed methods of rearing an albino strain of *Biomphalaria glabrata* and its parasites and studied mainly the interactions of *Paryphostomum segregatum* and *Schistosoma mansoni*. Certain redial species tended to be dominant, consuming stages of subordinate species. The main dominance characteristics of rediae included large size, possession of a mouth and a muscular pharynx. Thus, for example, *P. segregatum* could consume the smaller rediae of *Echinostoma lindoense* as well as schistosome sporocysts. They referred to this as direct antagonism. They also identified indirect antagonism, which occurs when parasite A retards the course of infection by B or leads to degeneration of B's stages. The mechanism for this sort of antagonism can still only be speculated upon. The notion of a dominance hierarchy for trematodes in snails, which assumes importance in later studies, had its origin largely in this work.

### Kill and dissect

Collecting snails to obtain data on trematode infections is a time-honoured and productive exercise for documenting the variety and frequency of multiple infections. A foundation study in this vein is that of Cort, McMullen & Brackett (1937) in



Table 1. Field infection profiles for some snail/trematode systems. Included are host species, total hosts examined, total trematode species found, number of infected hosts, and the number of double and triple infections observed. The number of species combinations is indicated in parentheses

Host snail	Number					Reference
	Examined	Species	Infected*	Double	Triple	
<i>Stagnicola emarginata</i> †	7259	17	4559	511 (25)	18 (9)	Cort <i>et al.</i> (1937)
<i>Cerithidea californica</i> ‡	12995	17	8680	667 (38)	23 (9)	Martin (1955)
<i>Cerithidea californica</i>	2910	10	448	13 (5)	0	Yoshino (1975)
<i>Cerithidea californica</i>	25854	15	5025	127 (33)	1	Sousa (1993)
<i>Ilyanassa obsoleta</i> ‡	5717	8	1467	52 (?)	0	Gambino (1959)
<i>Ilyanassa obsoleta</i>	5025	8	340	14 (?)	0	Vernberg <i>et al.</i> (1969)
<i>Ilyanassa obsoleta</i>	14978	6	614	0	0	McDaniel & Coggins (1972)
<i>Ilyanassa obsoleta</i>	11774	9	6010	1305 (16)	143 (7)	Curtis (1997)
<i>Velacumantus australis</i> ‡	1146	2	321	39 (1)	0	Ewers (1960)
<i>Velacumantus australis</i>	3842	4	1644	40 (?)	1	Walker (1979)
<i>Velacumantus australis</i>	8883	3	2221	165 (3)	1	Appleton (1983)
<i>Lymnaea stagnalis</i> †	1659	6	801	216 (6)	15 (3)	Bourns (1963)
<i>Buccinum undatum</i> ‡	1375	4	203	8 (2)	0	Koie (1969)
<i>Hydrobia stagnorum</i> ‡	16323	13	6128+	428 (17)	7 (3)	Vaes (1979)
<i>Planaxis sulcatus</i> ‡	4542	6	2053	192 (6)	1	Rohde (1981)
<i>Littorina littorea</i> ‡	2691	6	1152	88 (7)	0	Lauckner (1980)
<i>Helisoma anceps</i> †	4899	8	1485	69 (2?)	0	Fernandez & Esch (1991 a, b)
<i>Physa gyrina</i> †	1181	6	406	87 (7)	3 (2)	Snyder & Esch (1993)

\* with 1 or more species; consult reference; † freshwater; ‡ marine.

several Michigan lakes (Table 1). It was the first to find frequent multiple infections, including one quadruple. Curtis (1997) found 2 quadruple infections (1 species combination) in the estuarine *Ilyanassa obsoleta* (formerly *Nassarius obsoletus*). These are the only quadruples ever reported; infections of all species were patent and four is probably the limit for infracommunity species richness. Cort *et al.* (1937) were first to analyse frequency data to predict the number of multiple infections expected in a sample, assuming species combine at random (prevalence A × prevalence B × sample size = expected number of AB double infections in the sample). Observed and expected numbers of double infections were then compared. Most occurred about as expected, but some less often than expected (especially *Diplostomum flexicaudum* and *Plagiorchis muris*), suggesting barriers to coinfection.

Cort *et al.* (1937) did not use statistical analyses to compare observed and expected numbers of multiple infections. However, they noted that spatial (or temporal) heterogeneity in prevalence could affect expected numbers of multiples if samples from two or more sites (or times) were combined into one analysis. For example, if parasite A occurred only at site 1 and parasite B only at site 2, a combined-sample analysis would predict double infections. Nevertheless, A and B should not be expected to coinfect any snails.

Table 1 and Kuris & Lafferty (1994) identify a number of other important studies. For example, Martin (1955) dissected *Cerithidea californica*

(≥ 20 mm length) samples each month for a year from a small basin (~ 20 × 40 m) in Upper Newport Bay, California, a gathering point for shorebirds. Single and multiple infections were common. He commented that infection longevity might be conducive to multiple infections or that species may occupy different sites within the snail, making coexistence possible. Ewers (1960) tallied occurrences of *Stictodora* spp. and *Austroilharzia terrigalensis* in an estuarine snail in Australia. Using a random infection model, three times more double infections were observed than expected. He proposed that one species might predispose the snail to infection by the other and that snails eating faecal material from birds with multiple infections might also be involved. Bourns (1963) reported that multiple infections in *Lymnaea stagnalis appressa* in Ontario, Canada, often did not occur at random. Indeed, four combinations occurred significantly more often than expected. He suggested that, once infected by one species, predisposition to/against infection by other species, or inadequate sampling, might have produced his results. Koie (1969) studied a prosobranch along the Danish coast; double infections were few and she concluded they occurred at random. Vernberg, Vernberg & Beckerdite (1969) examined *Ilyanassa obsoleta* from Beaufort, North Carolina, first by observing cercarial emergence, then by dissection of infected snails. One sporocyst species, *Zoogonus lasius* (now *Z. rubellus*) was noted as being involved in many doubles. Another pair, *Himasthla quissetensis* and *Lepocreadium setiferoides* (both redial species, the former an echinostome),

were never observed together. They proposed that alterations in thermal acclimation patterns by one species prevented colonization by the other. Lim & Heyneman (1972) rejected this hypothesis in favour of direct antagonism. Yoshino (1975) found moderate prevalence and few double infections in *C. californica*, with the most abundant trematode being involved most frequently. He posited that the paucity of doubly-infected snails was due to direct antagonism. Multiple infections were rare in a *Hydrobia stagnorum* population, but Vaes (1979) saw little redial predation to explain it. Rohde (1981) concluded that species combined at random in an Australian coral reef snail. Lauckner (1980) presented original data on European *Littorina littorea*, observing that most doubles included *Himasthla elongata* and *Renicola roscovita*. Notably, there were no *Cryptocotyle lingua*-*H. elongata* doubles, even though both were frequent as single infections. Other species pairs also co-occurred rarely, others as expected.

Fernandez & Esch (1991a) studied infracommunities in the pulmonate *Helisoma anceps* in Charlie's pond (North Carolina). Most of the few double infections were *Halipegus occidualis* (redia) with *Haematoloechus longiplexus* (sporocyst). Laboratory observations established the dominance of *H. occidualis*. Nevertheless, it was concluded that spatial and temporal factors made such encounters rare in the host population and competition was seen as unimportant in structuring infracommunities. Snyder & Esch (1993) studied *Physa gyrina* in the same pond. Prevalence was similar, but many multiple infections were observed and dominance was not involved. In fact, congeners of the species that did not co-occur in *H. anceps* coexisted in *P. gyrina*. Based on these results, it can be stated that predictions regarding dominance based on taxonomic relatedness are not always reliable. Infracommunity differences in the two pulmonates were attributed to snail behaviour and factors external to the snails. Within-snail antagonisms were also considered of minor importance by Curtis (1997), who examined *Ilyanassa obsoleta* from nine sites in Delaware estuaries from 1981 to 1993. Prevalence ranged from 8.7 to 100%. Multiple infections were observed frequently at high prevalence sites. The sporocyst species, *Zoogonus rubellus*, *Gynaecotyle adunca* and *Austrobilharzia variglandis*, combined most frequently, both with each other and with redial species. Curtis (1995) has determined that *I. obsoleta* is long lived and, as a consequence, multiple infections are able to accumulate in the component community.

Statistical provision for spatial and temporal heterogeneity was made in a series of studies done on an estuarine snail (Kuris, 1990; Sousa, 1990, 1993; Lafferty, Sammond & Kuris 1994). A concern of these authors was whether heterogeneity or com-

petition within snails structure trematode communities. Kuris (1990) is influential in this regard. He proposed a method by which the importance of heterogeneity in generating expected frequencies of double infections could be dismissed or embraced. For example, suppose monthly samples have been collected from a given site. Using the random species combination approach, samples are analysed separately and monthly estimates of expected double infections are summed. Then, in another calculation, the total sample (all months combined) is analysed for prevalences and expected doubles. If the sum of monthly expected doubles is greater than expected doubles based on the total sample, then Kuris asserts the total sample analysis underestimates the expected number of multiple infections. Such an inequality would arise when prevalence of both parasites is simultaneously high in some months and low in others. If the sum of monthly expected values is smaller than the expected value based on the total sample, then the total sample analysis overestimates expected multiples. This could arise if prevalences of both parasites are independently variable among months. In either case, analysis of the combined sample would give a distorted expectation of double infections and heterogeneity is, therefore, deemed important. If expected doubles based on the sum of monthly samples equals the expected number based on the total sample, then Kuris says that heterogeneity 'may not be important'. The most clear-cut case would be when prevalences are identical in each month. There are, however, sets of variable prevalences among samples that encompass considerable heterogeneity yet yield nearly equal values. Accordingly, this outcome is equivocal. Mathematically, either expected value may be compared with the observed. However, biologically, it might still be better to recognize heterogeneity among samples. Kuris (1990) offered that, if heterogeneity can not explain the absence of doubles, then competitive exclusion in infracommunities must be the cause.

Kuris (1990) may well have a valid argument in a perfectly sampled world. However, any such analysis is based on the accuracy of prevalence estimates and these could easily be in error. For example, Curtis & Hurd (1983) and Curtis (1997), working with the estuarine *I. obsoleta*, found it difficult to collect representative samples. It was noted, for example, that a slight change in tidal elevation where samples are collected can change prevalences of certain species and, therefore, frequency of multiple infections. Thus, two samples collected in what is thought to be the same 'place' may actually be from different 'places'. Further, if the samples are collected at different times, they produce what is thought to be temporal heterogeneity when it is actually spatial. Reversat & Silan (1991) commented cogently, '... the distribution of this type of helminth is rarely uniform in host populations which are not

uniformly distributed either ...'. Sampling strategy must be wisely designed and we rarely possess sufficient knowledge of host/parasite biology to do this automatically.

Kuris (1990) used *Cerithidea californica* and erected a competitive dominance hierarchy for 15 trematodes that infect this species of snail. The hierarchy was based partly on sources of direct evidence. Snails were examined in the laboratory (for release of cercariae) and colour coded according to infecting species, then released, recollected at some later time and re-examined. If one species replaced another, or if a new species colonized an existing infection, this was taken to indicate dominance. Also, dominance was indicated if, on dissection, rediae of 1 species were observed consuming stages of another. Lines of indirect evidence for dominance included possession of rediae (especially if large), taxonomic relatedness, use of large rather than small snails, the gonad as the site of infection and site displacement. Basically, species with large rediae (*Parorchis acanthus*, *Himasthla rhigedana*) were high in the hierarchy and sporocyst species lower. Oddly, schistosome sporocysts, *Austrobilharzia* sp., could coexist with both dominant redial species, but in turn dominated only the poorest competitors.

With the establishment of the dominance hierarchy, Kuris (1990) estimated the impact of competition. Essentially, if A is dominant over B, snails infected by A were not available to be infected by B (corrected for any AB double infections); losses in B due to the presence of A in the component community could be estimated. Estimates of the percent of subordinate infections lost to competition ranged from 6 to 44%. He concluded that competitive interactions were an important structuring force for trematode communities.

Lafferty *et al.* (1994) developed this conclusion further for *C. californica* and Kuris & Lafferty (1994) extended it to other snail-trematode infracommunities. Whereas these papers addressed features of the component community, infracommunity competition was used as the basis to explain them. Lafferty *et al.* (1994) collected snails with a shell height of 25–30 mm (to reduce size heterogeneity) from 5 sites about 50 m apart over 20 days. The life span of *C. californica* is at least 7 years (Sousa, 1993) and these snails would have been several years old. Snails within sites apparently mingled at random and no movement between sites was assumed. Their model also assumed that many more double infections are present initially than are observed in samples of mature snails. They analysed for spatial heterogeneity effects (Kuris 1990) based on their model and concluded that combined samples would overestimate expected double infections, and that subordinate infections were lost to competitions based on their dominance hierarchy. They concluded

that competition within the infracommunity was the major structuring force for the component community. The model underlying this conclusion holds that first a flood of miracidia infects young snails, yielding many multiple infections; competition then occurs and many of these multiples are resolved into single infections. However, the rate at which trematodes actually colonize *C. californica* was not examined and this factor was not considered in their model. A high rate of parasite recruitment among young snails would be required to support the model. Unfortunately, little is known about the rate at which gastropods accumulate trematodes. The only studies directly addressing this issue are those of Sousa (1993), Curtis (1996), and Curtis & Tanner (1999), and results indicate that the rate of parasite recruitment is low.

Kuris & Lafferty (1994) performed a meta-analysis on 62 studies of larval trematodes in snails to see if competition in infracommunities structured these component communities. They erected dominance hierarchies for the sets of trematode species included based on published studies when available, then used taxonomic relationships and other indirect lines of evidence (Kuris, 1990) when not. The analysis included 296180 snails, of which 62942 were infected with one or more species of trematodes. Overall, they estimated that competition eliminated 13% of the infections and concluded it to be a potent structuring force.

Sousa (1990) looked at the component community of trematodes in *C. californica* at two sites in Bolinas Lagoon, California from 1981 to 1988. Recognizing the competitive hierarchy of Kuris (1990), he held that infracommunity interactions were partly responsible for the paucity of multiple infections. He concluded, however, that competition could not determine component community structure because new patches of juvenile snails are always available as a resource. Consequently, trematodes coexist in the component community even if they do not in infracommunities. Sousa (1993) paid more direct attention to the rarity of multiple infections and infracommunity dynamics. Spatial and temporal heterogeneity were deemed important and analyses were based on unaggregated samples. Because double infections were uncommon, Monte Carlo methods were used to estimate the likelihood of doubles being so rare. The analysis showed that multiples were rarer than expected. Pair-wise analyses revealed that individual species did not occur randomly in snails. Redial species tended not to co-occur; they also tended not to co-occur with sporocyst species, although a few did, notably when the schistosome *Austrobilharzia* sp. was involved. Moreover, sporocyst species tended to occur together, as predicted. Observations of *Himasthla*, *Parorchis* and *Echinoparyphium* rediae consuming co-occurring species during dissections were also

reported. Consistent with his earlier treatment, Sousa concluded that, whereas larval trematodes may interact negatively, coexistence in the host population is unaffected because there are always new hosts to infect.

#### Site displacement

Most infections in snails are by a single species that is adapted to occupy preferred sites, often in the gonad-digestive region. In multiple infections, when one species evicts another, distribution of the subordinate species must become progressively restricted until eliminated. One species may also displace another from its preferred site, but the two establish an equilibrium in the snail. These two situations would be difficult to distinguish based on a single observation.

DeCoursey & Vernberg (1974) examined *I. obsoleta* from North and South Carolina by dissection and histology. They found *Zoogonus rubellus* sporocysts often existed side-by-side with *Lepocreadium setiferoides* rediae, but *L. setiferoides* was occasionally displaced. *Austrobilharzia variglandis* appeared to occupy an abnormal site when co-occurring with *Cardiocephalus brandesii*, even though both were present throughout the snail. When the echinostome *Himasthla quissetensis* was present with *A. variglandis*, a few *H. quissetensis* rediae were displaced to sites nearer the head where some were degenerated to encapsulated. If these are consistent interspecific responses, they do not conform to expected dominance relationships since species with rediae, especially echinostomes, should dominate. Curtis & Hubbard (1993) viewed trematode spatial distribution in *I. obsoleta* in Delaware. They examined snail tissues microscopically and found that no species consistently displaced a co-occurring species. In most snails, '... all species present occurred throughout'. Although Vernberg *et al.* (1969) and Curtis (1985) reported that *H. quissetensis* and *L. setiferoides* never co-occurred, they were observed together in the study by Curtis & Hubbard (1993). When together, both were producing cercariae, but the latter species seemed the more vigorous infection.

Yoshino (1975) noted that certain trematode species in *C. californica* occupied the mantle and could coexist with species using the visceral spiral. Further, *Euhaplorchis californiensis* displaced a strigeid from the gonad to the digestive gland. He suggested that the locus of single infections may change with locality of the snail due to variability in the genetic strain of snail or parasite. Cheng, Sullivan & Harris (1973) also suggested this to be the case for *I. obsoleta*. Postulating local genetic variability is problematic when definitive host mobility and, with *I. obsoleta* planktonic larvae, are considered (Curtis & Hubbard, 1993; Gandon & Van Zandt, 1998).

Walker (1979) and Appleton (1983) found that *Austrobilharzia terrigalensis* only infects *Velocumantus australis* when the snail is already infected by another trematode and that it subsequently inhibits, but does not evict, the other species. They speculated that this trematode requires the host's tissues to be altered or the host's defences neutralized by the first infection before it can successfully colonize.

When *Echinoparyphium elegans* and *Schistosoma bovis* co-occur in the freshwater snail *Bulinus truncatus*, the latter's distribution appears to be extended (Mouahid & Mone, 1990). In *Biomphalaria pfeifferi*, Jourdan & Monkassa (1986) observed displacement of *Schistosoma mansoni* primary sporocysts to a deeper position in the snail foot when a dominant species, *Echinostoma caproni*, was also present. Sporocysts that were displaced survived whereas those remaining tended to degenerate. Movement to deeper tissues was interpreted as part of the competitive interaction between the two trematodes and coevolution was suggested.

#### Experimental infections (and redial habits)

Lim & Heyneman (1972) reviewed the basic work in this area and general findings are discussed in the introduction to this section. Here, we consider the following question. Does consumption by rediae represent an aggression toward individuals of another species for purposes of nutrition, i.e. is it predation *per se*, or is it simply opportunistic browsing? Sousa (1992) entertained the browsing hypothesis and rejected it because (1) rediae seldom consume their own kind, (2) they tend to attach actively to larvae of subordinate species, and (3) mobile rediae tend to aggregate where subordinates are concentrated. Alternatively, it is suggested that rediae are adapted to 'chew' their way through host tissues, and not to consume other trematodes. To this end, they have a mouth, often large size and a sucking pharynx. Moreover, rediae must be adapted to avoid consuming their own kind because it would be maladaptive to do otherwise. Finally, feeding on loosely attached germinal sacs of larval trematodes, especially where concentrated, may be easier than tearing off pieces of host tissue. Redial infections that grow faster in a coinfection (Lim & Heyneman, 1972) may be the result of easily-obtained nutrition. A key issue in deciding which hypothesis, e.g. directed competition through consumption of the other's stages or opportunistic browsing, is closer to the truth is whether the 2 trematode species in question encounter each other frequently enough in nature to respond to each other adaptively. Curtis & Hubbard (1993) noted that, even if multiple infections are quite common collectively, particular pairs seldom coexist. It is thus conceivable that consumption of stages of other species by rediae is a



by-product of the manner in which rediae are adapted to interact with the host rather than a direct response to another species of trematode.

#### *Interspecific interaction with cercariae output*

A snail presumably represents a limited resource and one infecting species may affect another in terms of how many cercariae are produced. If frequent enough, this could have ecological and evolutionary consequences. The conundrum is that this effect would best be measured in the field, which is problematic given the usual rarity of multiple infections.

DeCoursey & Vernberg (1974) studied cercariae production by 10 *I. obsoleta* in the laboratory every 3 hours for 27 hours, enumerating cercariae produced by *Zoogonus rubellus* alone, *Lepocreadium setiferoides* alone, and in combination. Single infections produced a mean of ~3500 cercariae, whereas in double infections a reduction was suggested; *Z. rubellus* released ~900 and *L. setiferoides* ~1500. Curtis & Hubbard (1993) also measured cercarial production in *I. obsoleta* in a variety of single ( $n = 162$ ), double ( $n = 134$ ), and triple ( $n = 65$ ) infections involving *Himasthla quissetensis*, *L. setiferoides*, *Z. rubellus* and *Gynaecotyle adunca*. Variability in cercarial production was high. A downward trend in output from multiple infections was often seen, but it was not significant. When in combination, these larval trematodes thus do not appear to consistently affect one another.

#### *Species composition changes*

Snails can be tested for infection by cercarial release and marked, then released in the field, recaptured later and re-examined. Workers with freshwater snails generally seem confident that release of cercariae will accurately reflect patent infections, although prepatent infections will certainly be missed (Goater *et al.* 1989). Results of Curtis & Hubbard (1990) suggest that, in marine snails at least, caution must be exercised in interpreting release of cercariae. When individuals of *I. obsoleta* were tested in field containers, 59.1% of determinations proved to be erroneous on later dissection. Errors were most frequent among multiply infected hosts.

Fernandez & Esch (1991 *a*) reported that *Helisoma anceps* in Charlie's Pond (North Carolina) had few double infections among their marked snails, but were able to observe parasite recruitment as well as loss of active infections (see also Goater *et al.* 1989), sometimes being replaced by other species. Sapp & Esch (1994) used *H. anceps* and *Physa gyrina* caged in the field to test whether interspecific trematode interactions dictated infracommunity structure. Into

one set of cages were placed five uninfected and marked *H. anceps* and *P. gyrina*. In another set of enclosures were placed *H. anceps* experimentally infected with *Halipegus occidualis*. It was not possible to experimentally infect *P. gyrina*. Cages were positioned at various depths and distances from shore, as these factors had been shown to affect parasite recruitment. Placing enclosures at least 5 cm from the bottom of the pond prevented colonization by egg-transmitted species, e.g. *H. occidualis* and *H. eccentricus*, the 2 most common parasites in the pond. This manipulation did not affect infracommunity structure as there was no significant difference between prevalence of infections with miracidia-transmitted species in caged and uncaged snails. In effect, there was no competitive release and colonization was unaffected by the absence of common species.

Curtis (1996) released 1400 individually marked and uninfected *I. obsoleta* on Cape Henlopen (Delaware) to study colonization by trematodes. These sentinels were released into an area with high prevalence (~80%+) of infected snails. Of 185 sentinels recovered, 2.7% had single-species infections. After correcting for infections that may have been undetected during initial screening, he concluded that the colonization rate was 1.6% yr<sup>-1</sup>. This result, coupled with the long life spans of hosts and their infections (Curtis, 1995), led him to conclude that time, not competition, was the most important factor in development of trematode infra- and component communities in this snail.

Sousa (1993) tracked 1170 previously infected *C. californica* for up to 4 years. Of the snails released, 1.5% recruited an additional species and 6.3% switched infections. *Himasthla rhigedana* and *Parorchis acanthus*, dominant trematodes in the Kuris (1990) hierarchy, were responsible for >90% of these changes. It is a matter of judgement, but this number of infection changes in snails exposed to new infections for such a considerable time seems modest. Curtis & Tanner (1999) examined colonization of *I. obsoleta* in Delaware. They released 300 marked natives (most of which were infected) onto Cape Henlopen, and 249 uninfected snails and 231 natives (virtually all infected) at Savages Ditch in nearby Rehoboth Bay. Only 16 initially uninfected snails were recovered over three summers and two had become infected; their estimate for colonization rate at Savages Ditch was 6.3% yr<sup>-1</sup>. This was higher than on Cape Henlopen (Curtis, 1996), but was based on many fewer snails and still quite low. Their final conclusions about changes in infection status among natives involved a number of considerations, but ultimately they asserted that six of 123 (4.9%) recovered natives (both sites) had changed infection status over periods ranging up to 3 years. Based on all evidence to date, species composition changes appear infrequent.

*Interactive versus isolationist infracommunity debate*

Holmes & Price (1986) developed the concepts of isolationist and interactive parasite communities. They stated that '... competition must be demonstrated as a process and any inference about past evolutionary change through competition must be approached with extreme caution'. We would add that attributing pervasive *ecological* importance to interactions requires equal caution. Demonstrating intra- or interspecific competition requires identifying a limiting resource, or competitive release in the absence of interaction, or both. The theatre of interaction is the individual host and frequent colonization is a primary requirement for interactive communities. New species must be recruited often and must then compete for limited resources. In contrast, low colonization rate is a primary feature of isolationist communities.

The debate about whether parasite infracommunities are interactive or isolationist has rarely been centered on larval trematodes in snails. Certainly in the view of Kuris (1990), Lafferty *et al.* (1994) and Kuris & Lafferty (1994), competition is important and infracommunities are interactive. Sousa (1994) also considered the issue and pointed out that since infections reproduce asexually, infrapopulations are almost always dense. He went on to state that snails offer a limited number of target organs to infect and that there is much evidence that species interact antagonistically when they co-occur. He concluded that 'infracommunities of larval trematodes have the potential to be strongly interactive' and that colonizations of snail hosts from definitive hosts 'are spatially and temporally variable, as are the rates of interspecific interaction among intramolluscan larval stages'. Infracommunities can thus be interactive or isolationist at different times and places, which is probably close to the reality of the matter.

Sousa (1993), Curtis (1996) and Curtis & Tanner (1999) are the only studies to address trematode colonization rate in snails explicitly and all suggest rates are low. The latter two investigations were done in habitats where trematode prevalence was very high and multiple infections frequent. If competition between species is to be frequent, then it should occur under these conditions. However, Curtis & Tanner (1999) observed that, even if species composition changes occurred at a posited rate of 10% yr<sup>-1</sup>, it would mean that, on average, an infracommunity might see a new species interaction once in 10 years. *Ilyanassa obsoleta* is long lived and snails with the same infection 3 years running (now 5; Curtis, unpublished observation) have been documented. These infracommunities likely persist long enough for a change to occur, but an interactive situation is clearly not indicated. In freshwater systems, however, many snails are short lived and

trematode communities are reset as snail generations turnover annually, or even more frequently (Esch & Fernandez, 1994). Perhaps miracidia colonize snails at higher rates in freshwater. If so, given the widely observed tissue-consumptive behaviour of rediae, freshwater infracommunities should be more interactive. However, data on colonization rates in the field seem not to exist. Further, Fernandez & Esch (1991*a*), Snyder & Esch (1993) and Sapp & Esch (1994) all held interspecific interactions to be unimportant. In a marine system, Curtis & Hubbard (1993) and Curtis (1997) worked with abundant multiple infections and noted that particular species co-occur infrequently, with time being the important factor in the accumulation of infections. Are trematode infracommunities in snails interactive or isolationist? We think, as does Sousa (1994), they potentially can be interactive. However, to be so requires high colonization rates which, to date, have not been demonstrated. It is probably best to operate under the null hypothesis that they are isolationist until there is substantive field evidence to the contrary.

## THE COMPONENT COMMUNITY

*The spatial landscape*

Spatial effects on trematode component community structure in snails can be examined through a landscape ecology approach. Landscape ecology is concerned with four general properties (Turner, 1989): (1) spatial heterogeneity and how it changes over time; (2) biotic and abiotic exchanges across heterogeneous areas; (3) how heterogeneity affects biotic and abiotic processes; and (4) managing or preserving spatial heterogeneity. Landscape ecology is not new to parasitology, dating back to Pavlovsky's (1966) work (landscape epidemiology) on the distribution of parasitic disease across large areas. However, the techniques and concepts widely used today in landscape ecology have been developed most profusely in the last couple of decades (Sokal & Oden, 1978; Burrough, 1981; Gardner *et al.* 1987; Milne, 1988; Tilman, 1994; Gustafson, 1998).

In a very general sense, a landscape is any heterogeneous or patchy area (With, 1994; Burke, 1997). Though the traditional focus of landscape ecology has been on relatively large areas, encompassing many ecosystems, the approaches and methods are also applicable at much smaller spatial scales. This is useful for parasite ecology because parasites are nested within a hierarchical framework, i.e. the infra-, component, and compound communities. At the largest scale, the species pool of trematodes from which local communities are drawn is called the regional pool. Within a region, there are a number of (more or less) distinct ecosystems; this is the local scale and roughly equivalent to the

Table 2. Distribution of trematode species in *Ilyanassa obsoleta* from nine collecting sites in and around Delaware Bay (from Curtis, 1997)\* × = present; – = absent

Parasite	Site								
	CH	CN	CC	IR	BB	GM	CS	SD	TI
<i>Lepocreadium setiferoides</i>	×	×	×	×	×	×	×	×	×
<i>Zoogonus rubellus</i>	×	×	×	×	×	×	×	×	×
<i>Himasthla quissetensis</i>	×	×	×	×	×	×	–	×	–
<i>Stephanostomum tenue</i>	×	×	×	×	–	×	×	–	–
<i>Stephanostomum dentatum</i>	×	×	×	×	×	–	–	–	–
<i>Gynaecotyla adunca</i>	×	×	×	×	–	–	–	×	–
<i>Austrobilharzia variglandis</i>	×	×	×	×	–	–	–	–	×
<i>Pleurognius malaclemys</i>	–	×	×	–	–	–	×	–	–
Unknown	×	×	–	–	–	–	–	–	–
<i>Diplostomum nassa</i>	×	–	–	–	–	–	–	–	–

\* Index of nestedness =  $10.54^\circ$  ( $P = 0.0003$ ) based on 'temperature' method of Atmar & Patterson (1993).

compound community. Within each local ecosystem, snail populations, as well as the infective stages of trematodes, are likely to be non-randomly distributed among habitats and habitat types, with some degree of exchange among habitats. At a smaller scale (microgeography of Esch & Fernandez [1994]), snails represent patches of habitat (Sousa, 1993) and infective stages represent patches of propagules. At the smallest scale considered here are processes that might occur within an infected snail, e.g. competition.

*Regional scale.* The species richness of any trematode component community cannot exceed the upper limit imposed by the regional species pool. Deviations from local areas harbouring all regional species are thought to occur by two processes. First, there is always an element of chance involved in determining the species present in any local community; recruitment is determined by dispersal history and local extinction. Second, a series of biotic and abiotic characteristics in local systems may set a limit to the species richness and composition, either through deterministic interspecific interactions, or through the pattern of spatial covariance of critical resources for each individual community member, or some combination of both.

As suggested earlier, interspecific interactions among trematodes in snails may affect community structure (Kuris, 1990; Fernandez & Esch, 1991a; Kuris & Lafferty, 1994; Lafferty *et al.* 1994), but do these processes provide power of prediction at the regional scale? Studies by Lafferty *et al.* (1994) and Curtis (1997) address this question because their work is the result of dedicated effort within single regional species pools. Curtis (1997) surveyed the trematode parasites of *I. obsoleta* occurring at nine sites in and around the Delaware Bay and found strikingly different communities at each of the sites. The data in Table 2 suggest that the pattern of trematode occurrence on this regional scale is nested

among local areas and, although other factors could be involved, that definitive hosts might occur among these sites in a nested pattern. In contrast, the Lafferty *et al.* (1994) study on *C. californica* at five sites on the California coast does not reveal a nested pattern of trematode species composition (Table 3), even though species richness and composition are still rather variable among sites. The absolute scales of investigation in these two studies are rather different, encompassing many km in the Delaware investigation and less than a quarter of a km in California. Nonetheless, at both scales, variety in species composition is the striking pattern.

Studies that incorporate direct observations on the occurrence, much less the abundance, of definitive host taxa are absent on a regional scale. Definitive hosts for trematodes range from the rather locally-restricted fishes to broad-ranging and mobile birds and mammals. Although a number of null hypotheses could be tendered for the study of regional determinants of species richness and composition, the most logical and simple one is that definitive host distributions determine the entire pattern.

*Local scale.* Rarely can an entire ecosystem, say a pond or estuary, reasonably be considered as a homogeneous environment. Critical resources are neither uniformly nor randomly distributed within local systems. Again, detailed studies regarding the distribution of all hosts in trematode life cycles are largely absent at this scale. However, a number of independent, if not directed, attempts have been made to account for the manner in which spatial heterogeneity affects trematode component community structure at this scale.

The investigation by Bartoli & Holmes (1997) illustrates how spatial heterogeneity can affect transmission, and thus abundance, of trematodes in a snail population. Shown in Fig. 1 are redrawn distributions of the spatial coincidence of the hosts in

Table 3. Distribution of trematode species in *Cerithidea californica* from five collecting sites on the California coast (from Lafferty *et al.* 1994)\* × = present; – = absent.

Parasite	Site				
	2	3	4	1	5
<i>Euhaplorchis californiensis</i>	×	×	×	×	×
<i>Himasthla rhigedana</i>	×	×	×	×	×
<i>Parorchis acanthus</i>	×	×	×	×	–
<i>Echinoparyphium</i> sp.	×	×	×	×	–
<i>Acanthoparyphium spinulosum</i>	×	×	×	–	×
Cyathocotylid	×	×	–	×	×
Small xiphidiocercaria	×	×	×	–	–
<i>Renicola buchhanani</i>	×	–	–	–	×
Large xiphidiocercaria	–	–	×	–	–

\* Index of nestedness =  $10 \cdot 29^\circ$  ( $P = 0 \cdot 107$ ) based on 'temperature' method of Atmar & Patterson (1993).

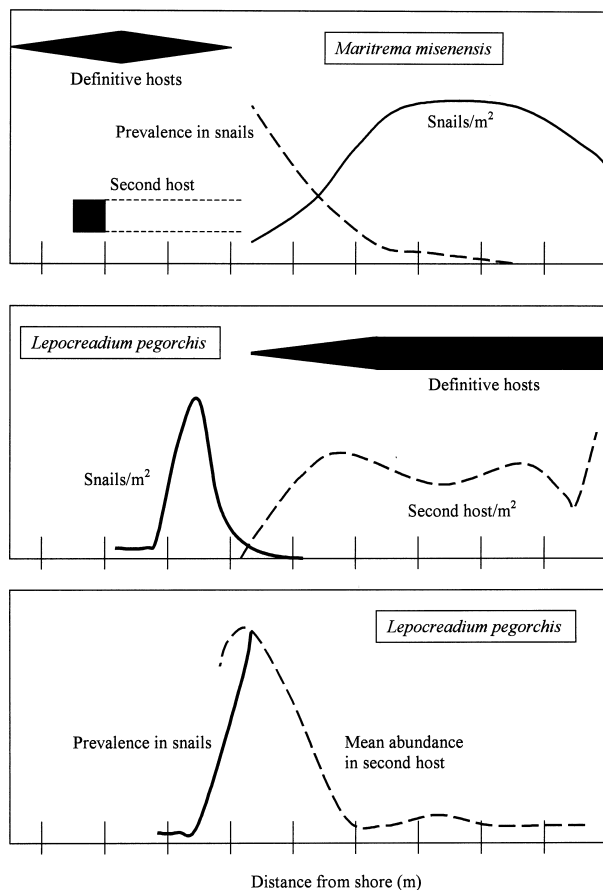


Fig. 1. Distribution of host populations for 2 trematodes, *Maritrema misenensis* (top panel) and *Lepocreadium pegorchis* (middle and bottom panels), along a transect in the Mediterranean Sea off France. Redrawn from Bartoli & Holmes (1997).

the life cycles of two trematodes occurring in two different snail species along a 150 m transect in the Mediterranean waters off France. For both *Maritrema misenensis* and *Lepocreadium pegorchis*, the definitive hosts and the second intermediate

hosts co-vary in a strong, positive manner with respect to spatial distributions. The snails are, however, somewhat negatively associated with the other two hosts in the life cycle. In neither case are these trematodes most prevalent in snails where snails are most dense, rather the focus of infection in snails appears to be determined by areas of spatial overlap of the host populations.

The lesson to be garnered from these observations is that spatial constraints to transmission definitely exist within ecosystems, indicating a way in which structure might be purveyed to trematode component communities. As Bartoli & Holmes (1997) point out, small-scale investigations provide an appropriate window through which constraint on parasite transmission can be viewed. Incorporating such a landscape approach to understanding trematode component communities is a most exciting prospect for future investigations involving these systems.

Many studies document spatial heterogeneity in the richness and species composition of trematode communities in snails at a local level (Appleton, 1983; Curtis & Hurd, 1983; Williams & Esch, 1991; Sapp & Esch, 1994). Snails themselves respond to various environmental stimuli (Harman, 1972; Okland, 1983), producing aggregated distributions among habitats or habitat types, or both. Furthermore, the diversity of snail species both in freshwater and marine environments ensures that a number of different habitat preferences will be represented in an ecosystem. For instance, Laman, Boss & Blankespoor (1984) studied the depth-distributions of seven species of snails in Douglas Lake, Michigan and found striking differences among the snails present, with most species distributed unimodally but differing in the depths at which they were most dense. Such systems in which detailed knowledge of snail distributions are known provide excellent opportunities to determine



whether these patterns influence the spatial structure of the trematode component communities.

Curtis & Hurd (1983) demonstrated a sharp boundary in the parasite community structure along the Cape Henlopen sandflat occupied by *I. obsoleta*. In one zone, snails harboured six species of trematodes but in an adjacent zone, only two trematodes were present. Parasitism increased with shell height for snails from both zones; however, in the zone with greater species richness, parasitism was significantly higher in medium-sized snails than in the zone with low species richness. These data suggest that definitive host distributions among these areas were responsible for the differences in trematode species richness among snail sub-populations. Sapp & Esch (1994) gathered point-in-space data for each 1231 *Physa gyrina* and 1532 *Helisoma anceps* collected over a year in Charlie's Pond, North Carolina. Overall prevalence of parasitism in *H. anceps* was negatively associated with water depth where the snails were collected (Williams & Esch, 1991). The same result was observed for overall parasitism in *P. gyrina*, as well as a significant effect of snail size and distance from shore. Individual species of trematodes in this system differed in their relationships with habitat characteristics where snails occurred. The limited mobility of these snails, together with their short life spans (< 1 year for *H. anceps*; about 3 months for *P. gyrina*), makes these point-measures of habitat use particularly important. In more vagile and longer-lived snails, point-measures are less likely to be as informative.

Appleton (1983) examined the prevalence of three trematodes in *Velacumantus australis* at 14 sites in the Swan estuary, Australia. Trematode species richness varied from zero to three among these sites. In general, prevalence of these trematodes was negatively associated with water turbulence and velocity, which Appleton (1983) attributed to the terrace profile of the sites, in addition to the positive effect of aggregating avian definitive hosts in areas sheltered from incoming tides. Bowers (1969), Cannon (1979), James (1968), and Threlfall & Goudie (1977) all found that trematode infections were concentrated in a limited area of the host snail's range, defined by vertical zonation and likely caused by the aggregation of definitive hosts. Appleton's (1983) work also revealed that prevalence of infection in *V. australis* for each trematode was related unimodally to snail density, such that lower-medium densities of snails were associated with the highest levels of infection, whereas extremely dense groups of snails and extremely sparse groups of snails were less heavily infected. This observation is reminiscent of Bartoli & Holme's (1997) work described earlier. Jokela & Lively (1995) found *Microphallus* sp. infections in *Potamopyrgus antipodarum* to be highest in shallower habitats, whereas *Telogaster opisthorchis* was more prevalent in deeper habitats. Prevalence in

a number of rarer trematodes was apparently not related to water depth, and was independent of *Microphallus* sp. infection in *P. antipodarum*. Jokela & Lively (1995) attributed these differences to definitive host behaviour as well.

The emerging theme from these studies of spatial variation in trematode prevalence and component community structure within single ecosystems is one of spatial constraint on transmission from definitive hosts. The complexity of spatial patterns among parasites that can require three or more host organisms during their life cycle could be overwhelming (see first section of this paper). Nevertheless, we think detailed studies at the local level, incorporating data on definitive hosts, snails, other intermediate hosts and habitat characteristics are particularly useful because they provide instant predictions that can be tested by moving to another compound community. Different ecosystems in a region will be characterized by different physical, chemical and biological properties and, thus, provide the requisite variation in putative structuring forces discovered at the local level to test the generality of the model at more regional levels. This protocol, i.e. intensive study in one ecosystem followed by broadening to a regional level, is an approach that could be utilized to determine how space and spatial structure affects trematode component communities, but it has not yet been employed.

Landscape ecology among trematodes in snails, as well as many other parasites, has a second, equally important facet. All organisms modify their environment to some extent. Trematodes, however, not only modify their immediate habitat (snails), they also can affect the positioning of that habitat in an ecosystem. The known cases in which a trematode infection results in altered snail behaviour seem to centre upon, in a functional sense, the bridging of spatial constraints imposed by non-overlapping host distributions. Thus, when considering the effects of spatial heterogeneity on component community structure, it is not always enough to know where all the hosts are, but also if their spatial texture is influenced by the presence of a trematode.

Curtis (1987, 1990) found that *I. obsoleta* infected with *Gynaecotyla adunca*, migrated up onto beaches and sandbars during periods preceding low tides, especially night-time low tides. Semi-terrestrial crustacean beachhoppers, which are the second intermediate host, are most active at night and occur on the beach head. Uninfected *I. obsoleta*, or snails infected with other species of trematodes, do not exhibit this behaviour. Curtis (1987, 1990) interpreted this parasite-induced altered snail behaviour as an adaptation to increase the probability of contact between beachhoppers and cercariae from the snail. During a series of observations, many *G. adunca*-infected snails were seen to make multiple migrations up the beach head, suggesting that this modified

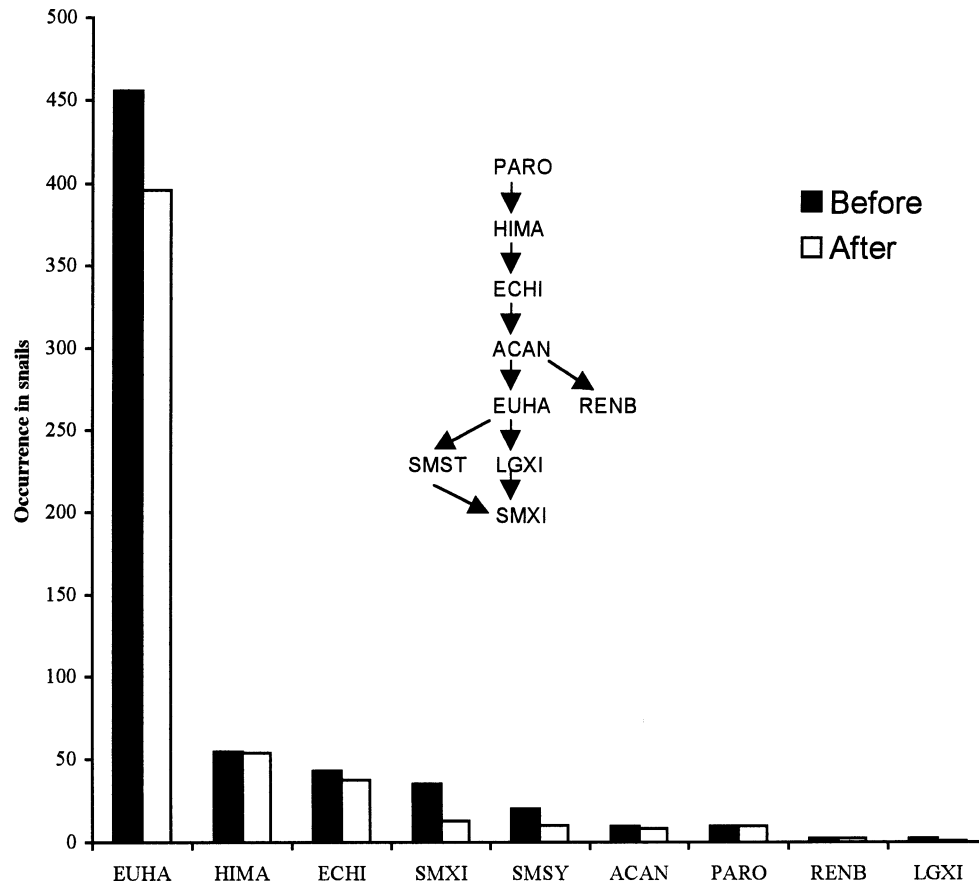


Fig. 2. Abundance of trematodes (number of snails infected) in *Cerithidea californica* as observed (after) and as estimated prior to the effects of competitive exclusion (before). Dominance hierarchy of trematodes shown in inset. Data taken from Lafferty *et al.* (1994).

behaviour is sufficiently complex to allow tracking of tidal cycles. Furthermore, shedding of cercariae is restricted to night-time at low tide. *Gynaecotyla adunca* occurs frequently in multiple infections (Curtis, 1987, 1997), but how these form and why is unknown. Sindermann (1960) found that infection of *I. obsoleta* with a variety of trematodes tended to reduce inshore to offshore migration during the fall, when uninfected snails typically move to low tide zones to overwinter. Movement of snails from deep water to shallow water in spring is coincident with avian definitive host behaviour of *Austrobilharzia variglandis*, providing spatial overlap of the two hosts in the life cycle. Thus, with the *I. obsoleta* system there are examples of different species of trematodes differentially affecting behaviour of the same snail, although each of these responses results in essentially the same microhabitat use.

*Infracommunity scale.* Because an entire section of this review has already been dedicated to infracommunities, we will not revisit any of the details here. It is clear, however, that the topic of interspecific interactions among trematodes has received a lion's share of recent focus among researchers in

this field. There is no doubt that these interactions occur and that deterministic outcomes are the result when two trematodes infect the same snail. But, there is no clear consensus on the importance of these interactions at larger scales.

Studies of competition demonstrate that habitat patchiness is sufficient to result in coexistence of competitors that exclude each other at the local (patch) level (Tilman, 1994). Generally, some trade-off is necessary, whereby inferior competitors require dispersal abilities greater than superior competitors for coexistence to be permanent over long time-scales. Although it is conceivable that a superior competitor could have sufficient dispersal ability as to saturate all patches and thus exclude all inferior competitors, no such system has been found in parasitic or free-living systems. Thus, contrary to the original 'paradox of diversity', a focus on spatial patchiness and heterogeneity has resulted in a new paradigm, i.e. diversity is the null hypothesis because patchiness and heterogeneity are ubiquitous. The original non-spatial models of competition (Lotka-Volterra) are not incorrect, they simply apply only at the infra-patch level. Only if the superior competitor is ubiquitous among habitat patches and (at least)

dynamically permanent in all patches, do the non-spatial models apply at the “meta”-community level (component community for parasites). Thus, the expectation is that infracommunity-level competition will not be a controlling factor on component communities because of the patchiness of the habitat in which competition occurs. This prediction is supported for all trematode communities in snails that have been studied to date. There is no evidence that interspecific trematode interactions result in exclusion of a trematode species from an ecosystem. This is no doubt due to the overwhelming effect of constant egg input into the systems by wide-ranging definitive hosts and that snails are an abundant and renewable resource.

Competition in individual snails can, however, modify the prevalence of inferior competitors in a snail population. Lafferty *et al.* (1994) estimated that 16% of observed single infections in *C. californica* were actually the result of a resolved coinfection, with species-specific effects ranging from 1.7% to 63.4%, and the most inferior competitors suffering the greatest percentage losses in patch occupancy. However, the overall pattern of abundance relationships among trematode species (community structure) was not seriously altered by competition (Fig. 2). If competition ‘scales-up’ as a determinant of community structure, it should affect processes (and therefore patterns) at larger scales. It is rare when a trematode component community consists of a superior competitor that also is the most abundant (prevalent) in the assemblage, although there is considerable variation. We know of no case where relative abundances of trematodes in a snail component community are ordered representations of a dominance hierarchy such as that proposed by Kuris (1990) for trematodes in *C. californica*.

Sousa (1993), for instance, found that at Kent Island, California, the two most prevalent trematodes in *C. californica*, *Parorchis acanthus* and *Himasthla rhigedana*, are also the most dominant in the hierarchy. At Pine Gulch Creek, these two species were less prevalent than only the third most competitively dominant trematode *Echinoparyphium* sp. On the other hand, in the study by Lafferty *et al.* (1994) in a different area, *Euhaplorchis californiensis*, fifth in the dominance hierarchy of seven levels, was far and away the most prevalent trematode in *C. californica*, averaging over five sites as 41 times more prevalent than *P. acanthus* (1st in the dominance hierarchy), over 7 times more prevalent than *H. rhigedana* (2nd), and over 10 times more prevalent than *Echinoparyphium* sp. (3rd). *Helisoma anceps* in Charlie’s Pond (North Carolina) were most often infected by *Halipegus occidualis*, which is positioned in the middle of the dominance hierarchy of trematodes in this system (Fernandez & Esch, 1991a, b). The two most competitively dominant trematodes, both echinostomatids, were orders-of-

magnitude less abundant than *H. occidualis*. Similarly, Sapp & Esch (1994) reported that *H. occidualis* occurred at a peak prevalence of 59.5% in *H. anceps*, whereas the remaining species, including the dominant *Echinostoma* sp., were much less prevalent (this echinostome peaked at approximately 6% in prevalence).

It does not appear as though knowledge of a dominance hierarchy produces much predictability among local areas. Prevalent trematodes in one ecosystem may be relatively rare in other ecosystems, apparently independent of competitive ability at the infracommunity level. There may be a trade-off in most local systems between position in the competitive hierarchy and prevalence, thereby ensuring coexistence of trematodes. Whether this trade-off has evolved or is simply happenstance is a matter requiring study. Differences in trematode abundance relationships among systems likely are reflections of the abundance of definitive hosts, intermediate hosts, or both, rather than reflections of competitive ability. Whereas all large-scale patterns and processes necessarily affect smaller-scale patterns and processes, the reverse is not always true. Interspecific interactions can have controlling effects on overall community structure, e.g. keystone predator (Paine, 1966). The interspecific interactions among trematodes in snails, with the results to date, is not one of the systems in which this occurs.

### *The temporal landscape*

The temporal landscape is not fundamentally different from the spatial landscape except in being a single dimension rather than three. The questions essentially are the same, e.g. how is this dimension used by each species in the community and what effect does this pattern of utilization have on patterns and processes at higher and lower levels of organization?

The longevity of snails in a population, coupled with the longevity of trematode infrapopulations, should determine the degree to which a component community is susceptible to seasonal and year-to-year vagaries. The component communities of short-lived hosts (multiple cohorts per season) should be influenced more by processes changing over ecological time-scales than in long-lived hosts (multiple seasons per cohort). This draws an obvious dichotomy between marine and freshwater systems. Marine prosobranchs live for several years to several decades, whereas the majority of freshwater pulmonates live for a few years at most. Freshwater prosobranchs fall somewhere in the middle, having life spans that can approach a decade. In temperate freshwater systems, seasonal variation in the input of trematode eggs to a system is canonized; less is known about the dynamics of egg production and

release among adult trematodes in marine vertebrates.

Short-lived hosts might be expected to harbour distinct component communities throughout a single season if the trematodes use definitive hosts with temporally localized breeding and/or activity seasons, e.g. a spring community followed by an autumn community. Twin infection peaks in trematode parasitism have been reported for a number of snails (Probert, 1966; references in Esch & Fernandez, 1994). However, these are largely due to the life history of the snail, i.e. mortality and larval recruitment, although the ephemeral nature of allogenic (those requiring a host outside, and usually ephemeral to, the ecosystem) parasites also is a factor. Snyder & Esch (1993) studied the seasonal dynamics of the component community of *P. gyrina* in Charlie's Pond. Over the summer, *P. gyrina* continually reproduces, such that cohorts are so broadly overlapping that no change in trematode component community composition was observed. Furthermore, most of the definitive hosts in this system are fairly persistent throughout the entire summer; only *Echinostoma* sp., an allogenic trematode, was temporally restricted during the summer. As pointed out previously, Curtis (1996) estimated that the probability of *I. obsoleta*, which lives for decades, recruiting a trematode on the Cape Henlopen sandflat was 1.6% over the summer months. Given that overall prevalence among native snails at Cape Henlopen is around 80%, this value suggests slow accumulation of infections over the 30 or more year life span of this snail and effectively eliminates seasonality as a factor in the temporal landscape.

The probability of local extinction should be one of the most striking factors determining the structure of a component community over time. In general, autogenic trematodes (those completing their life cycles within a single ecosystem) should have lower probabilities of local extinction than allogenic trematodes. Thus, trematodes of migratory birds and wide-ranging mammals may be expected to appear and disappear from local component communities, depending on the movement of their hosts from season to season. Over the course of many years and numerous studies in Charlie's Pond, the trematodes of migratory waterfowl have experienced the greatest local turnover rates (Schotthoefer, 1998). These local extinctions have been associated with the trematode species that otherwise would be the most competitively dominant in the component community of *H. anceps*. In this way, temporal factors are likely to affect the prevalence of interspecific antagonism in infracommunities as well as overall species richness and composition. During the same time period, an autogenic trematode of *P. gyrina* in Charlie's Pond, *Halipegus eccentricus*, also became locally extinct sometime around 1996, and has

remained absent from Charlie's Pond since (Schotthoefer, 1998). Autogenic species, which should be more persistent locally, also are less likely to recolonize an ecosystem once local extinction has occurred. Thus, within a regional species pool, and subject to the constraints imposed by local conditions, trematode component communities may be expected to reach a dynamic equilibrium of species richness and composition determined by the values of dispersal and extinction for autogenic and allogenic species (Esch & Fernandez, 1994).

The component communities of long-lived snails should be more resistant to local extinction if trematode infections are rather permanent at the infracommunity level. Even ephemeral visitation by definitive hosts should result in long-term persistence of a trematode in a system where the snail lives for decades and infection with that trematode can persist as long as the snail is alive. Utilizing trematodes in snails as indicator species in long-lived and short-lived snails has variable connotations. A well-done, short-term survey of the trematodes in a long-lived snail should reveal long-term relationships among all the hosts in each trematode life cycle. For instance, Curtis & Tanner (1999) posited that trematode infrapopulations in *I. obsoleta* persist unchanged, on average, for about 10 years. Thus, a survey today of this snail should reflect events that occurred years ago and long-term study of the same snail population may not reveal seasonal differences. In contrast, short-lived hosts can be used as indicators of season-to-season differences in ecosystem-level interactions, e.g. visitation by migratory waterfowl.

The lack of long-term census and quantification of dispersal/extinction probabilities hinder any detailed account of whether the predictions outlined above are valid. The mosaic of hosts that trematodes require for their life cycles makes these parasites valuable indicators of ecosystem-level properties. At the same time, however, this same complexity makes quantification of trematode dynamics very difficult. For instance, the ability to colonize new ecosystems often is described as 'greater' for allogenic trematodes than for autogenic trematodes. Whereas undoubtedly true, this categorization is of little use when trying to place autogenic and allogenic trematodes on a probability continuum. Whether lumping all autogenic parasites and all allogenic parasites into single groups provides the necessary predictive power over longer ecological time scales will require dedicated study over several decades.

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