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A review of the influence of host- and parasite-related factors and environmental conditions on the host-finding capacity of the trematode miracidium

N. Ø. CHRISTENSEN

Summary

Methods for studying the chemosensitivity of the miracidium to the host snail comprise stereomicroscopical or photographic observations of miracidial behaviour in various types of experimental systems containing snails, snail material or snail-conditioned water. Studies on the influence of environmental factors on miracidial host-finding have primarily been conducted by assessment of infection rates among exposed snails, using either registration of intramolluscan stages or recording of cercarial shedding and by recently introduced radio-isotope assay systems.

The miracidial host-finding process represents a complex interplay between the physiological and behavioural activities of the snail and the miracidium. The process exhibits a sequential pattern due to adaptive miracidial responses to the snail host and to environmental stimuli. In phase I the photo- and geotactical responses of the miracidium induce a distribution within the environment which corresponds to that of the host snail. Phase II, the scanning phase, consists of a random movement within the host environment, and phase III, the final localization and penetration of the host snail, is governed by the chemosensitivity of the miracidium to the host. It is still discussed whether the miracidial response to the host is chemotactical or chemoklinokinetical, and conflicting opinions still exist concerning the nature of the responsible stimulant(s). The chemosensitivity of the schistosome miracidium exhibits a very low degree of specificity, while snail genera specificity and even a partial species specificity exists among miracidia of other species of trematodes.

The host-finding process is regulated by the combined effect of various physico-chemical and biological environmental conditions. Influential physico-chemical factors include water volume, water velocity, temperature, hydrogen-ion concentration, salinity and turbidity. Biological environmental factors of

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importance comprise the population densities of susceptible snails and interference with miracidial host-finding by non-susceptible snails and other aquatic organisms. Non-susceptible snails primarily interfere with miracidial host-finding due to the decoy effect (abortive or successful miracidial penetration into non-susceptible organisms) but other mechanisms such as accumulation of miracidia by filter-feeding is also of importance. Interference with miracidial host-finding by other aquatic organisms is due to predation, filter-feeding, secretion of miracidial toxins and the decoy effect.

Key words: miracidium; snail; *Schistosoma*; *Fasciola*; methodology; host-finding; photo- and geotactical responses; chemosensitivity; environmental factors.

Introduction

The snail-finding of the digenean trematode miracidium plays a vital role in the transmission of the parasite in that the continuation of the developmental cycle is directly related to the efficiency of the process. The host-finding process, which is regulated by environmental characteristics, takes place in complex aquatic habitats, characterized by variations in the levels of each of several physico-chemical and biological factors and by different permutations in the levels of the various factors.

The aim of the present review is to summarize current knowledge concerning the host-finding capacity of the digenean trematode miracidium in relation to host- and parasite-related factors and environmental conditions with special reference to the genera *Schistosoma* and *Fasciola*. Besides, experimental systems applied in studies on miracidial behaviour and ecology are described and evaluated, limitations in our present status of knowledge are pointed out, and proposals for further studies are outlined.

Chernin (1974) discoursed on the topic in a broad outline, but the huge number of relevant papers published since and the importance of dealing with the subject in some more detail calls for the need of reviewing the topic at its present stage.

Experimental systems applied in studies on miracidial ecology

A range of valuable experimental systems has been devised for studying the chemosensitivity of the miracidium to the host snail. Some of these systems are based on direct observations of miracidial behaviour in small wells "point-inoculated" with snail-conditioned water (Chernin, 1970), around agar blocks soaked with snail material (MacInnis, 1965) and in different types of choice systems (Kloetzel, 1958, 1960; Etges and Deerer, 1963; Plempel, 1964; Shiff, 1968; Shiff and Kriel, 1970; Roberts et al., 1978). Other systems employ dif-

ferent types of photographic techniques for scoring behavioural patterns, i.e. the flying spot microscope (Davenport et al., 1962), dark ground photography (Wilson and Denison, 1970; Mason and Fripp, 1976; Prechel and Nollen, 1979; Roberts et al., 1979) and microcinematography (Sponholtz and Short, 1975).

Studies on the host-finding capacity of the schistosome miracidium as such in relation to environmental conditions have primarily been conducted using registration of daughter sporocysts in the host snail 12–14 days after their exposure to miracidia in a given experimental system. This method, originally described by Chernin and Dunavan (1962) enables an objective evaluation of the host-finding capacity, but since no correlation exists between the number of daughter sporocysts and the number of penetrating miracidia, the method is non-quantitative. Upatham (1973a) modified the method and claimed this version to be quantitative, but later studies by Christie and Prentice (1978) and Wilson (personal communication) have not been able to confirm these findings.

Recording of cercarial shedding from exposed host snails has also been applied in the study of schistosome miracidial host-finding (e.g. DeWitt, 1955; Chu et al., 1966; Prah and James, 1977, 1978; James and Prah, 1978). This method is also non-quantitative, in that neither the establishment of the infection nor the size of the cercarial production can be correlated directly with the number of penetrating miracidia.

Studies on the host-finding capacity of the *Fasciola hepatica* miracidium have been conducted using registration of rediae in the host snail approximately 3 weeks following exposure (Wilson and Taylor, 1978), a method which is also non-quantitative, and by a radioisotope assay system described by Nansen and Frandsen (1974) and Christensen et al. (1978). This method involves exposure of the host snail *Lymnaea truncatula* to ^{75}Se -methionine labelled miracidia (Nansen et al., 1976a) under given experimental exposure conditions, followed by a registration of the subsequent amount of snail-bound radioactivity. In that a linear relationship exists between the amount of snail-bound radioactivity and the number of miracidia available in the exposure system (Christensen et al., 1978), the snail-bound radioactivity can be used as a quantitative measure of the host-finding capacity. A possible limitation of this method is the theoretical possibility of the existence of some influential environmental factors the effect of which is first reflected in a killing of post-penetrating larvae. However, experimental evidence for the existence of such factors is still lacking.

A corresponding radioisotope assay system for testing the host-finding capacity of the *Echinostoma revolutum* miracidium has recently been described by Christensen (1980), while methodological problems in miracidial labelling, i.e. a relatively low amount of miracidia-bound radioactivity and difficulties in removing free radioactivity from the miracidial suspension impose severe limitations in the possible application of this method in studies on the schistosome miracidium (Christensen et al., 1977a).

Apart from the above described methods sampling and counting techni-

ques (Yasuraoka, 1953, 1954; Takahashi et al., 1961) and photographic techniques (Wilson and Denison, 1970; Mason and Fripp, 1976) have also provided valuable information on miracidial speed of movement and distributional patterns in relation to physico-chemical conditions, but the ultimate relevance of such isolated observations to the matter of miracidial host-finding hinges to a large extent on interpretation.

Sequential pattern in the miracidial host-finding process

On the basis of mainly hypothetical considerations Wright (1959) originally proposed that the trematode miracidial host-finding process can be divided into three phases, a valuable suggestion later confirmed for the schistosome miracidium through a number of experimental studies conducted in the laboratory, under semifield conditions and in a few experiments in the field.

In phase I the schistosome miracidium responds to environmental stimuli such as light and gravity (photo- and geotactical responses) in a manner similar to the host snail with the result that the miracidia concentrate in that part of the environment where a suitable host is likely to be found (Chernin and Dunavan, 1962; Shiff, 1974), and daily or seasonal changes in the distribution of the host snail(s) may be accompanied by corresponding changes in miracidial behaviour (Takahashi et al., 1961; Shiff, 1974). Phase II, the scanning phase, consists of a random movement within the host environment, and phase III, the final localization and penetration of the host snail, is governed by the chemosensitivity of the miracidium to the host snail.

The sequential pattern described above does presumably also occur in the miracidial host-finding process of other species of trematodes but ultimate experimental evidence to support this assumption is not yet available.

Miracidial responses to environment and host controlling the host-finding process

The photo- and geotactical responses of the miracidium and its chemosensitivity to the host snail play a vital role in the host-finding process, and exemplify the importance of behavioural patterns and responses to the host for the level of efficiency of the host-finding of free-living larval parasites.

Photo- and geotactical responses of the miracidium

A huge number of laboratory studies have been conducted to describe various behavioural patterns of miracidia of various species of trematodes in response to light and gravity, among many others Yasuraoka (1953, 1954), Wilson and Denison (1970), Wright and Ronald (1972), Wright et al. (1972), and Mason and Fripp (1977), but the relevance of such observations on the microscope bench to the matter of host-finding is often questionable (see Wright, 1971). However, other studies conducted in the laboratory and under

semifield and field conditions have provided some, but still incomplete, information on the cooperation of the photo- and geotactical responses in the host-finding process, especially as far as the schistosome miracidium is concerned. Chernin and Dunavan (1962) and Upatham (1972a, b) showed that the *S. mansoni* miracidium is negatively geotactic and positively phototactic and in addition gravitates to the edges of shallow waterbodies, inducing a distribution of miracidia within the environment which corresponds to that of the host snail, *Biomphalaria glabrata*. Takahashi et al. (1961) and Shiff (1969, 1970, 1974) furthermore showed that the photo- and geotactical responses of the miracidium of *S. japonicum* and *S. haematobium*, respectively, alter with changes in temperature, inducing a behaviour (distribution) parallel to that of the respective host snails under similar conditions. In short, the negative photo-response of the *S. haematobium* miracidium reverses as temperature declines while a temperature increase alters the positive photo-response of the *S. japonicum* miracidium.

Besides giving some knowledge on miracidial host-finding these studies also suggest the need for further experimentation for obtaining more detailed information on behavioural patterns of miracidia of both schistosomes and other trematode species and also on behavioural ecology of the host snails before a complete understanding will be available. For example, Prah and James (1978) recorded successful host-finding by *S. mansoni* miracidia released at the water surface at a water depth of two meters which implies that their positive phototactical and negative geotactical responses may not be as absolute as described above.

The chemosensitivity of the miracidium to the host snail

A huge number of valuable experiments have been conducted to study various fundamental aspects of the chemosensitivity of the miracidium to the host snail, presumably due to its convenience as a model for studying behavioural parasitology. The topic has been reviewed recently by Ulmer (1971), Chernin (1974), MacInnis (1976) and Saladin (1979), and on this account basic aspects of the chemosensitivity will not be dealt with in detail in the present review. In short, it is generally agreed that the chemosensitivity of the miracidium plays a vital role in the final localization and penetration of the host snail (phase III) but it is still discussed whether the miracidial response is chemotactical or chemoklinokinetical, and conflicting opinions still exist concerning the nature of the responsible stimulant(s).

The specificity of the chemosensitivity of the schistosome miracidium seems to be rather low, and it has been concluded (e.g. see review by Basch, 1976) that intermediate host specificity in *S. mansoni* is not determined by a species-specific miracidial chemoresponse. Thus, Chernin (1970, 1972) demonstrated that the prepenetration behavioural changes (the exited stage) are induced by unsusceptible strains of *B. glabrata*, by a number of non-susceptible

species of snails of other genera and even by the oligochaete *Nais* sp. Besides, numerous reports exist on the penetration of the *S. mansoni* miracidium into non-susceptible species of snails, e.g. Cram et al. (1945), Stunkard (1946), Abbott (1948), Newton (1952), Brooks (1953), Barbosa and Barreto (1960), Sudds (1960), Richards (1963), Barbosa (1965), and even into tadpoles of *Phyllomedusa* sp. (Amphibia) (Barbosa and Carneiro, 1965). Besides, Sudds (1960) and Chernin and Perlstein (1969) observed abortive attempts to penetrate snails belonging to the genus *Helisoma*.

Genera- and species-specificity has, however, been demonstrated to exist for the *F. hepatica* miracidium. Thus, Nansen et al. (1976b) obtained indirect evidence for a genera specificity by showing that the penetration occurs into various snail species of the genus *Lymnaea*, but not into various other snail species belonging to the families Lymnaeidae Physidae and Planorbidae (Basommatophora), and Hydrobiidae and Valvatidae (Prosobranchia). Other studies by Christensen et al. (1976a) have shown that this presumably is due to a lack of attraction of the miracidium to snails other than *Lymnaea* sp. Direct evidence for a partial species-specificity was obtained by Neuhaus (1953) and Christensen et al. (1976a), who demonstrated a clear preference of the *F. hepatica* miracidium for the host snail *L. truncatula* over other species of the genus *Lymnaea*.

Snail- and parasite-related factors influencing the host-finding process

Snail physiology and "immunity"

The final establishment of the contact between the miracidium and the susceptible snail host (phase III) is in principle influenced by the physiological activity of both the snail and the miracidium. Anderson (1978) and Carter (1979) recently pointed to the possible importance of genetic heterogeneity within the snail population on the frequency distribution of miracidia among the snails and on the resulting level of parasitization. However, studies by various authors, i.e. Chernin and Dunavan (1962), Shiff (1968), and Carter (1979) suggest that at least populations of schistosome host snails seem to be relatively homogeneous in their susceptibility to miracidial penetration, i.e. that failure rates reflect miracidial peculiarities and not some quality of the individual snail.

Preliminary, but convincing experimental evidence for the importance of the physiological status of the host snail for the establishment of the host/parasite contact was obtained by Chernin (1970) who demonstrated that *B. glabrata* conditioned water produced at a temperature of 4° C is not able to induce the exited stage of the *S. mansoni* miracidium when tested at 20° C. Although being preliminary, this observation points to the need for further work to clarify these important aspects of the miracidial host-finding.

Homologous and heterologous "resistance" in larval trematode infections

in the snail host, including the possible development of initial barriers to miracidial penetration, have been dealt with in a huge number of recent experimental studies. In recent reviews by Lim and Heyneman (1972) and Basch (1976) it has been concluded that no barriers to penetration of the schistosome miracidium develop as a result of a primary homologous or heterologous infection in the host snail. Christensen et al. (1976c) extended these observations by showing that *L. truncatula*, harbouring primary infections with *F. hepatica* in various stages of development do not develop barriers to further homologous miracidial penetration.

Miracidial physiology

Among others, Chernin and Antolics (1975) have shown that a certain proportion of newly hatched *S. mansoni* miracidia, usually 25–30%, in close confinement to susceptible snails is not able to penetrate. This figure is relatively high as compared with other species of trematodes, i.e. *F. hepatica* (Christensen, unpublished data) and might as suggested by Chernin (1974) reflect the high degree of contact (physiological, immunological) between the egg-shell enclosed schistosome miracidium and the tissues of the final host before getting access to the freshwater environment.

The physiological activity of the miracidium, which is governed by the combined effect of the physico-chemical conditions of the environment, is reflected in the speed of movement, in the length of the infective period and in the penetrative capacity as such. The combined effect of speed of movement and the length of the infective period determines the scanning capacity, which is defined as the area (volume of water) which the miracidium can search still retaining the ability to penetrate and infect the host snail.

Incorporated glycogen in limited amounts is the main source of energy during the free-living stage of the miracidium (Bryant and Williams, 1962) and declining speed of movement at increasing age, as demonstrated by Wilson and Denison (1970) and Mason and Fripp (1976) for the *F. hepatica* and *S. mansoni* miracidium, respectively, reflects a decline in available glycogen (Wagner, 1965; Bruce et al., 1971). Wilson and Denison (1970) and Mason and Fripp (1976), respectively, demonstrated an increasing rate of movement of the *F. hepatica* and the *S. mansoni* miracidium at increasing temperatures resulting in the commonly observed declining miracidial longevity at increasing temperature. However, such observations are of limited value in that motility (longevity) is in general retained for a longer period than infectivity (e.g. Upatham, 1972c) and in that most of such longevity studies have been conducted under poorly defined experimental conditions.

Attempts to determine the length of the infective period under controlled experimental conditions seem to be limited. Chernin (1968) showed that the infectivity of the *S. mansoni* miracidium at room temperature is unaltered for 7 hours after hatching followed by a decline. Prah and James (1977) confirmed

these findings and obtained a corresponding figure for *S. haematobium*. Prah and James (1977) furthermore demonstrated that the infective period of both the *S. mansoni* and *S. haematobium* miracidium is longer at moderately low than at high temperatures. Indirect evidence for a shortening of the infective period of the *F. hepatica* miracidium at high temperatures was obtained by Wilson and Taylor (1978), while direct evidence was obtained by Christensen et al. (1976b) who demonstrated that the penetrative capacity of the *F. hepatica* miracidium is unaltered for 7 hours at moderately high temperature and for 24 hours at 8° C.

Physico-chemical environmental factors influencing the host-finding process

A huge number of experimental studies have been conducted to elucidate how physico-chemical environmental factors influence miracidial host-finding, but precautions must be taken in the interpretation of some of the results obtained. Thus, most studies have been conducted in simplified experimental systems with too close a contact between miracidia and snails, neglecting the crucial fact of testing both the penetrative potential and the scanning capacity. Furthermore, nearly all studies have dealt only with the separate effect of each individual factor and not with the decisive combined effect of the various factors.

Water volume and water velocity

Studies on the host-finding capacity of the schistosome miracidium in relation to water volume, water depth and water velocity have been conducted by Chernin and Dunavan (1962), Shiff (1968, 1969), Upatham (1972a, b, c, 1973a), and James and Prah (1978), while Wilson and Taylor (1978) studied the effect of variations in snail densities on the host-finding capacity of the *F. hepatica* miracidium. Based on the results obtained it can be concluded that the ability to locate the host snail is in general being reduced at increasing water volume, at increasing water depth, at increasing water velocity, and at decreasing snail densities. The maximum horizontal distance recorded for successful host-localization in standing water is 9.14 m for *S. mansoni* (Upatham, 1973a) and 5.1 m for *S. haematobium* (James and Prah, 1978). The maximum water depth recorded for successful host-location is for both *S. mansoni* and *S. haematobium* 2 m (Prah and James, 1978). Based on these and other studies (Upatham, 1972b) it has been concluded that water depths normally encountered in the host snail habitats present no barrier to schistosome miracidial snail-finding.

Various results have been obtained concerning the influence of water velocity on schistosome miracidial host-finding, but Shiff (1968), Upatham (1973a), and James and Prah (1978) agree that host-location can occur at flow rates at or below 10 cm/sec, while successful host-finding is rare above this level.

Upatham (1973a) recorded successful host-finding by the *S. mansoni* miracidium at a distance of 97.54 m downstream in moderately flowing water, and Webbe (1966) and Upatham (1973a) have concluded that moderately flowing water increases the scanning capacity of the schistosome miracidium.

Temperature

The lower temperature level for the infection of the host snails by miracidia of both *S. mansoni* and *S. haematobium* when being in close contact with the snails seems to be 15–16° C (DeWitt, 1955; Upatham, 1973b; Prah and James, 1977) while the optimum temperature level for both species seems to be 25–34/35° C (Upatham, 1973b; Prah and James, 1977). The corresponding figures for *F. hepatica* miracidial host-finding are 5–6° C and 15–26° C, (Christensen et al., 1976b). Christensen et al. (1976b) furthermore demonstrated that the host-finding process of the *F. hepatica* miracidium is slowed down at 10° C and 13° C, but that the final level of efficiency is identical to that at optimum levels, and that the blockage below 5–6° C is reversible when increasing the temperature. Thus, the earlier described increase in the length of the scanning period of the *F. hepatica* miracidium at moderate low temperatures may to a certain extent compensate for the reduced host-penetration capacity at these temperatures. This assumption stresses the importance of testing both the penetration potential and the length of the scanning period.

Hydrogen-ion concentration

Upatham (1972c) demonstrated that pH levels below 6 and above 9 reduce the infectivity of the *S. mansoni* miracidium while Christensen et al. (1978) showed that the ability of the *F. hepatica* miracidium to penetrate the host snail (close confinement) is unaltered within the pH range of 5.4–8.4, but reduced at a pH of 8.9.

Salinity

Upatham (1972c) showed that the infectivity of the *S. mansoni* miracidium decreases curvilinearly at increasing levels of NaCl until 4200 ppm, above which level no infections occur, while Chernin and Bower (1971) and Christensen et al. (1978) in close contact between miracidium and snail observed an unaltered “infectivity” of the *S. mansoni* and *F. hepatica* miracidium up to 2.39‰ and 3.79‰, respectively, followed by a progressive reduction at higher levels.

Turbidity

Upatham (1972c) and Christensen et al. (1978), respectively, found that the host-finding capacity of the *S. mansoni* and the *F. hepatica* miracidium is reduced in water with high turbidity levels.

Biological environmental factors influencing the host-finding process

Molluscs

The numerous earlier quoted observations of abortive or successful miracidial penetration into non-susceptible snails and into host snails already harbouring primary homologous or heterologous trematode infections (the decoy effect) give indirect evidence for a possible interference with miracidial host-finding, and this has in fact been amply proven in a number of recent experimental studies conducted in the laboratory, under semifield conditions and in the field. Table 1 presents a list of molluscs shown to interfere with miracidial host-finding and the mechanisms involved.

As appears in the Table most molluscan interference with miracidial host-finding is due to the decoy effect. However, the interference with *F. hepatica* miracidial host-finding by the bivalve *Sphaerium corneum* (Sphaeriidae) and the prosobranch *Bithynia tentaculata* (Hydrobiidae) is due to accumulation of miracidia by their filter-feeding activities (Nansen et al., 1976b).

Besides the information given in Table 1, Chernin and Perlstein (1969) and Christensen et al. (1977b) found that faeces, mucus and other secretions from the host snails do not interfere with the host-finding capacity of the *S. mansoni* and *F. hepatica* miracidium, respectively.

Other organisms

A number of experimental studies have clearly shown that several species of other aquatic organisms may also exercise a significant interference with miracidial host-finding (see Table 2). This interference is mainly due to predation and filter-feeding, but secretion of miracidial toxins (Turbellaria) and a decoy effect (amphibian tadpoles) have also been shown to be responsible.

Conclusion

Although a considerable biological insight is available concerning the influence of environmental and snail- and parasite-related factors on miracidial host-finding, a number of important questions still remain unanswered, and it is still fruitless to speculate on the precise limits imposed by such factors on natural transmission. The vast majority of studies have been conducted in the laboratory in simplified experimental systems making it impossible to evaluate the effect on both the penetration potential and on the scanning capacity of the miracidium. Besides, nearly all studies have dealt only with the separate effect of each individual influential factor and not with the decisive combined effect of the various factors. Further studies must therefore be conducted in more complicated laboratory systems and under semifield or field conditions making possible an evaluation of the combined effect of the various physical, chemical and biological environmental factors. Sturrock and Upatham (1973) have laid

Table 1. Species of molluscs interfering with miracidial host-finding

| Species of trematode | Species of mollusc | Mechanism of interference | Type of experiment | Author |
|----------------------------|---|---------------------------|--------------------|------------------------------|
| <i>Fasciola hepatica</i> | <i>Lymnaea palustris</i> | Decoy | Laboratory | Christensen et al. (1976a) |
| | <i>L. pereger</i> | Decoy | Laboratory | Christensen et al. (1976a) |
| | <i>L. stagnalis</i> | Decoy | Laboratory | Christensen et al. (1976a) |
| | <i>Bithynia tentaculata</i> | Filter feeding | Laboratory | Christensen et al. (1976a) |
| | <i>Sphaerium corneum</i> | Filter feeding | Laboratory | Christensen et al. (1976a) |
| <i>Schistosoma mansoni</i> | <i>Biomphalaria glabrata</i> (unsusceptible strains) | Decoy | Laboratory | Chernin (1968) |
| | <i>Bulinus truncatus</i> | ? | Laboratory | Chernin (1968) |
| | <i>Helisoma caribaeum</i> | Abortive penetration | Laboratory | Chernin and Perlstein (1969) |
| | <i>H. anceps</i> | Abortive penetration | Laboratory | Chernin and Perlstein (1969) |
| | <i>Marisa cornuariitis</i> | ? | Laboratory | Chernin (1968) |
| | <i>Drepanotrema surinamensis</i> | Decoy | Semifield | Upatham (1972d) |
| | <i>Lymnaea palustris</i> | ? | Laboratory | Chernin (1968) |
| | <i>Polypylis hemisphaerula</i> | ? | Laboratory | Chernin (1968) |
| | <i>Physa marmorata</i> | Decoy | Semifield | Upatham (1972d) |
| | <i>Pomacea glaucus</i> | Decoy | Field | Upatham and Sturrock (1973) |
| | <i>P. australis</i> | Decoy | Field | Upatham and Sturrock (1973) |
| | <i>Tarebia granifera</i> | Decoy | Laboratory | Laracuenta et al. (1979) |
| | | Decoy | Laboratory | Laracuenta et al. (1979) |

Table 2. Species of organisms other than molluscs interfering with miracidial host-finding

| Species of trematode | Species of organism | Mechanism of interference | Type of experiment | Author |
|----------------------------|---|---------------------------|--------------------|---|
| <i>Fasciola hepatica</i> | <i>Daphnia pulex</i> (Cladocera) | Filter feeding | Laboratory | Christensen et al. (1977b) |
| | <i>Corethra</i> sp. larvae (Diptera) | Filter feeding | Laboratory | Christensen et al. (1977b) |
| | <i>Planaria</i> sp. (Turbellaria) | Toxins | Laboratory | Mattes (1936)* |
| <i>Fasciola gigantica</i> | <i>Chaetogaster limnaei</i> (Oligochaeta) | Predation | Laboratory | Khalil (1961)* |
| <i>Schistosoma mansoni</i> | <i>Chaetogaster limnaei</i> (Oligochaeta) | Predation | Laboratory | Coelho (1957)*, Michelson (1964), Wajdi (1964)* |
| | <i>Athya innocuous</i> (Copepoda) | Predation | Field | Upatham and Sturrock (1973) |
| | <i>Cyclops</i> sp. (Copepoda) | Predation | Laboratory | Courmes et al. (1964)* |
| | <i>Culex pipiens</i> larvae (Diptera) | Filter feeding | Laboratory | Chernin and Perlstein (1971) |
| | <i>Aedes aegypti</i> larvae (Diptera) | Filter feeding | Laboratory | Chernin and Perlstein (1971) |
| | <i>Dugesia tigrina</i> (Turbellaria) | Toxins | Laboratory | Chernin and Perlstein (1971) |
| | <i>Dendrocoelum lacteum</i> (Turbellaria) | Toxins | Laboratory | Etges et al. (1975) |
| | <i>Planaria</i> sp. 4 species (Turbellaria) | Toxins | Laboratory | Glaudel and Etges (1973)* |
| | <i>Lebistes reticulatus</i> (guppy fish) | Predation | Semifield | Upatham (1972d), Bunnag et al. (1977) |
| | <i>Bufo marinus</i> tadpoles (Amphibia) | Decoy | Field | Upatham and Sturrock (1973) |
| | <i>Phyllomedusa</i> sp. tadpole (Amphibia) | Decoy | Semifield | Upatham (1972d) |
| | <i>Utricularia</i> sp. (plant species) | “Predation” | Field | Upatham and Sturrock (1973) |
| | | | Laboratory | Barbosa and Carneiro (1965)* |
| | | | Laboratory | Gibson and Warren (1970)* |

* indirect evidence by the recording of uptake of immobilization of miracidia

the basis for such further studies by showing that quite minor variations in pH and turbidity may enhance the adverse effect of increasing salinity on *S. mansoni* miracidial host-finding.

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