REVIEW ARTICLE

Aquatic molluscs as auxiliary hosts for terrestrial nematode parasites: implications for pathogen transmission in a changing climate

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SUMMARY

Nematodes are common parasites of molluscs but are often overlooked. Both metastrongyloid and rhabditoid species dominate the fauna within land snail and slug populations. Nevertheless, a key characteristic of many laboratory studies is the ability of these terrestrial nematodes to utilize aquatic molluscs as auxiliary hosts. The significance of this to the ecology of the parasite has never been evaluated. There is increasing concern as to the impact of climate change on the epidemiology of many parasitic diseases. In particular, it has been suggested that host switching may increase under the pressure of extreme climatic conditions. It is therefore timely to assess the role that aquatic molluscs may play in transmitting terrestrial nematodes, which include species of medical and veterinary importance such as *Angiostrongylus cantonensis*, *A. vasorum*, and *Muellerius capillaris*. The present review assesses the mechanisms of terrestrial nematode transmission through aquatic molluscs focusing on metastrongyloid and rhabditoid species, the importance of variable susceptibility of molluscan hosts, field studies on natural occurrence within aquatic habitats, and the impact of extreme climatic events (floods and droughts) that may increase in frequency under climate change.

Key words: molluscs, metastrongyloids, rhabditoids, auxiliary host, freshwater snails, *Angiostrongylus*, *Muellerius*, *Phasmarhabditis*, *Steinernema*, climate change.

INTRODUCTION

Parasitism of molluscs by nematodes is widespread, but compared to trematode infections is often overlooked. In particular, terrestrial gastropods are commonly infected with a wide range of species, although those of medical and veterinary importance such as *Angiostrongylus cantonensis*, *A. vasorum*, and *Muellerius capillaris* receive the most attention. Nematodes form a diverse range of parasitic associations with molluscs (Grewal *et al.* 2003) with increasing evidence to suggest that they may have an important role in regulating host population dynamics (Morand *et al.* 2004). Although there are many described parasite species only 2 major groups, metastrongyloids and rhabditoids, dominate the fauna. Metastrongyloids use molluscs as intermediate hosts, maturing in a vertebrate; in contrast, rhabditoids utilize only the mollusc to complete their life cycles (Grewal *et al.* 2003).

The nature of nematode development in molluscs is dependent on their life cycles, which are particularly varied (Grewal *et al.* 2003). In general, metastrongyloids that use molluscs as intermediate hosts enter the host as a first stage (L1) juvenile and develop up to a third stage (L3), further development requiring transmission to the vertebrate definitive host (Grewal *et al.* 2003). In contrast, where molluscs act as definitive hosts many different kinds of life cycles occur. It is often the case for rahabditoids that either juvenile stages develop in the host with a free-living adult or the entire nematode life cycle is completed within the mollusc. In some associations, death of the host is required to complete the life cycle with rhabditoid nematodes releasing symbiotic bacteria as a food source that multiply rapidly, and produce an endotoxin that kills the host within a few days allowing the nematode to develop on the cadaver (Grewal *et al.* 2003). Some species are capable of adopting different life cycles depending on the environmental conditions. For example, *Phasmarhabditis hermaphridita* is a facultative parasite that can reproduce in slug faeces and other organic-rich material or infect a mollusc and form a parasitic or necromanic relationship (Rae *et al.* 2007).

Many terrestrial nematode species are characterized by the wide range of molluscan species that can act as host (Grewal *et al.* 2003). One aspect of this generalist specificity is the ability to use aquatic

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molluscs as hosts under both natural and experimental conditions. Indeed, because aquatic molluscs demonstrate a high physiological compatibility with terrestrial nematodes and can be relatively easily cultured they have been widely used as laboratory hosts for studies on parasites of medical and veterinary importance such as *A. cantonensis* (Table 1). Nevertheless, both biological and ecological studies indicate that terrestrial snails and slugs are clearly the principal hosts utilized by these nematodes under natural conditions with aquatic molluscs acting as auxiliary hosts (*sensu* Dogiel, 1964). Typically, hosts of this kind are classified as having infection levels (prevalence, intensity, and abundance) that are lower than the principal host(s). Nevertheless, occurrence can vary greatly in auxiliary hosts, which may be due to ecological rather than phylogenetic conditions (Poulin, 2005). For example, one of the most important factors influencing specificity is the contact between parasite and host, particularly the behaviour of free-living stages (Dogiel, 1964). Under the influence of environmental change and the associated degradation of preferred habitats host switching by parasites may increase (Brooks and Hoberg, 2007). Nematode parasites of insects have a well-established capacity to utilize a wide-range of diverse auxiliary host species (Poinar, 1989; Bathon, 1996). However, the significance of aquatic molluscs as auxiliary hosts for terrestrial metastrongyloid and rhabditoid nematodes, with the notable exception of *A. cantonensis*, has been largely overlooked and the implications for parasite ecology never evaluated. In particular, under climatic extremes such as floods and drought, which can have devastating effects on land snails and slugs, aquatic molluscs may play a more prominent role in parasite transmission. The frequency of these kinds of extreme environmental conditions is predicted to increase under climate change (Morand and Guegan, 2008). It is therefore the aim of the present article to assess the role of aquatic molluscs in transmitting terrestrial nematode parasites and how climatic conditions may influence their status as hosts in the future.

LIFE CYCLES OF TERRESTRIAL NEMATODES THROUGH AQUATIC MOLLUSCS

Viability of free-living stages in water

The life cycles of many nematode species in aquatic molluscs have been elucidated under laboratory conditions. The first-stage larvae of metastrongyloids leave the definitive host with faeces and remain free living until they locate a suitable molluscan host. They do not feed, relying on energy reserves and consequently their survival is dependent on a range of environmental factors (Boev, 1975). Rhabitoides, in contrast, have a free-living adult which produces larvae that develop into an L3 dauer, a non-feeding stage infective to molluscs which, like metastrongloid larvae, may have to survive a long time under varying environmental conditions before encountering a compatible molluscan host (Morand *et al.* 2004).

Metastrongyloidea L1 have a high survival rate over many months in freshwater (Boev, 1975; Kontrimavichus *et al.* 1976; Kontrimavichus and Delyamure, 1979). Changes to the water's environmental condition can affect L1 viability. For example, increasing temperature gradually reduces survival, whilst infectivity peaks at an optimum temperature before declining (Skorping, 1982; Shostak and Samuel, 1984; Lorentzen and Halvorsen, 1986), However, the response to temperature varies between species, probably related to their different geographical distributions and the climatic conditions encountered there (Cabaret *et al.* 1991). Survival in seawater has also been documented but with a reduced activity and, on return to freshwater, infectivity to molluscs remains unaffected (Richards and Merritt, 1967).

Rhabditoid L3 can also survive for weeks in fresh water although they demonstrate a gradual decline in infectivity (Lewis *et al.* 1995; Grewal and Grewal, 2003). Changes in temperature, salinity, UV light and hypoxia can all affect viability of larvae in water (Thurston *et al.* 1994; Grewal *et al.* 2002; Grewal and Grewal, 2003). Nevertheless, 'fitness' varies considerably between individual species, possibly related to foraging strategies, which incur different metabolic demands. Survival is related to declining energy reserves; however, metabolic rates increase drastically after a few weeks in water. This may be due to osmotic stress, as the cuticle becomes more permeable with age and consequently osmoregulation is more difficult, ultimately leading to death (Lewis *et al.* 1995). The nature of the relationship between nematode and symbiotic bacteria also changes after prolonged periods in water. The number of viable bacteria declines after a few weeks, but varies between individual nematode species possibly because of differences in the way bacteria are stored in the host, which can affect both bacterial viability and their availability as a food source (Lewis *et al.* 1995).

Infection of aquatic molluscs

Nematodes are known to infect aquatic molluscs in 2 ways, either being accidentally ingested by the snail and penetrating through the intestinal wall or, less commonly, by direct penetration of the molluscan tegument. Direct penetration is a widespread mechanism of infecting terrestrial molluscs but appears difficult for aquatic species to accomplish (Yousif and Lammler, 1977). This is probably because few juvenile nematodes can produce body waves of the amplitude and frequency needed to achieve real swimming (Clark, 1994) and consequently they are unable to actively locate, attach, and penetrate a target host. Aquatic molluscs therefore acquire an infection mainly by accidental contact with larvae with little evidence to suggest that terrestrial nematodes can chemotactically locate hosts in water (Banevicius *et al.* 2006). Nevertheless, some species of freshwater pulmonates demonstrate water-leaving behaviour (Green *et al.* 1992) and it is possible that under natural conditions snails could become infected by direct penetration during periods spent on the banks of aquatic habitats.

A range of factors can influence the establishment of nematodes within molluscs. These include size/age of the host, density of larvae that snails are exposed to, age of the larvae, length of the exposure period, and temperature (Boev, 1975; Yousif and Lammler, 1975*a*; Li *et al.* 1986; Morley and Moritt, 2006). However, large variations in the response of individual host-parasite associations occur with few generalizations. For example, smaller/younger hosts have been found to be more susceptible to *A. cantonensis* and *M. capillaris* (Boev, 1975; Yousif and Lammler, 1975*a*; Solomon *et al.* 1996*a*). In contrast, the size/age of the mollusc had little impact on the infectivity of some protostrongylids (Cabaret, 1987). For terrestrial molluscs, at least, the relative importance of this factor appears to be associated with the species of host under exposure with some demonstrating higher susceptibility in older/larger snails whilst others demonstrate the opposite (Cabaret, 1987). Similarly, for the rhabditoid *P. hermaphridita* infecting *L. stagnalis*, smaller snails demonstrate a greater susceptibility than larger ones (Morley, unpublished observations).

Development of larvae in molluscs

Having penetrated into the molluscan host, larvae undergo further development. The rate of growth and maturation of nematodes is controlled by temperature. Increases in temperature cause a more rapid parasite development (Boev, 1975; Ishii, 1984). Many species, however, have a minimum temperature threshold for development, below which the parasite becomes dormant. Such a threshold varies between species and appears to be related to their geographical distribution. For example, *A. cantonensis*, a tropical species, has a minimum temperature threshold of approximately 15 °C (Ishii, 1984; Lv *et al.* 2006) whilst *M. capillaris*, a temperate species, develops down to 5 °C in terrestrial molluscs (Rose, 1957). In contrast, the subarctic species *Elaphostrongylus rangiferi* will only develop down to a 10 °C threshold. This is an adaptation to minimize larval mortality during winter because developing L2 and L3 have a higher mortality rate than non-developing L1 in the over-wintering snail host (Schjetlein and Skorping, 1995).

Development rates can vary depending on the species of mollusc infected. For example, *A. cantonensis* develops more quickly in *Lymnaea palustris* than *Biomphalaria glabrata* (Rachford, 1976*a*) whilst greater numbers of *P. hermaphridita* developed to L4 stage in *L. stagnalis* compared to *Physa fontinalis* after 14 days post-exposure (Morley and Morritt, 2006). In addition, the site of infection within the host can also influence parasite development due to local fluctuations in the availability of nutrients (Svarc and Zmoray, 1974).

In contrast, aestivation of the molluscan host does not appear to interfere with the development of nematode parasites (Gerichter, 1948; Richards, 1967), although it progresses at a slower rate than in active molluscs (Boev, 1975; Solomon *et al.* 1996*b*). This may be because in the aestivating host there is a decline in available nutrients and oxygen uptake which may suppress parasite metabolic activity as well as a build-up of snail excretory by-products which may inhibit larval growth (Solomon *et al.* 1996*b*).

Pathology of infection to molluscs

A number of patho-physiological changes occur in molluscs infected with metastrongyloid nematodes. Larvae cause localized damage to surrounding tissue and are usually encapsulated by the host (Harris and Cheng, 1975*a*, *b*; Rachford, 1976*b*; Hourdin *et al.* 1990). Changes in the dimensions of nerve ganglia as well as neural lesions have also been reported in infected molluscs (Szmidt-Adjide *et al.* 1996) possibly related to parasite-associated tissue necrosis (Hourdin *et al.* 1990). Specific studies on *Angiostrongylus* spp. show that infected molluscs have higher, but fluctuating, oxygen uptake rates (Rachford, 1976*c*) with levels of haemolymph glucose and calcium, but not protein, significantly reduced immediately following nematode infection (Brockelman, 1978; Brockelman and Sithithavorn, 1980; Stewart *et al.* 1985). However, after a few weeks of infection, levels of haemolymph glucose and enzymes, as well as digestive gland glucose, are significantly elevated compared to controls (Stewart *et al.* 1985). These increases may be associated both with glycogen breakdown in the foot muscle, the main site of infection, where tissue glucose levels are significantly reduced and additional tissue destruction caused by the emergence of mature larvae from the snail (Stewart *et al.* 1985).

Cellular responses to metastrongyloid nematode infections can be classified as either focal or generalized proliferative reactions and appear similar in both terrestrial and aquatic molluscs. The intensity and structure of focal responses depend to some extent on the type of tissue in which the larvae are localized but, regardless, eventually lead to encapsulation of the parasite (Yousif *et al.* 1980; Hourdin

Table 1. Species of aquatic molluscs determined to be viable hosts for terrestrial nematode parasites under experimental and natural (N) conditions

Nematode species	Aquatic molluscan intermediate host	Definitive vertebrate host (if applicable)	Reference
Order Strongylida			
Aelurostrongylus abstrusus	*Biomphalaria glabrata*	Cat	Wallace and Rosen (1970)
A. pridhami	*Ampullaria cupina, Gyraulus crista, G. deflexus, Physa integra*	Mink	Anderson (1962)
Angiostrongylus andersoni	*Lymnaea stagnalis, Planorbarius corneus*	Rodents	Petter (1974)
A. cantonensis	*Ampullarium canaliculatus* (N), *Bellamya aeruginosa* (N), *B. ingallsiana* (N), *B. quadrata* (N), *Biomphalaria alexandrina* (N), *B. glabrata* (N), *B. heliophila, B. obstructa, B. pallida, B. pfeiferi, B. straminea, B. tenagophila, Bulinus africanus, B. contortus, B. forskalii, B. globosus, B. senegalensis, B. tropicus, B. truncatus* (N), *Cipangopaludina chinensis* (N), *C. malleata, Cleopatra bulimoides* (N), *C. cyclostomoides* (N), *Crassostrea virginica, C. rizophorne, Drepanotrema simmonsi, Ferrissia tenuis, Galba viridis, Goniobasis livescens, Gyraulus hiemantium, Helisoma* sp., *Indoplanorbis exustus* (N), *Lanistes carinatus* (N), *Lymnaea* sp. (N), *L. cailliaudi* (N), *L. columella, L. japonica, L. natalensis* (N), *L. ollula, L. palustris, L. stagnalis, L. swinhoe, L. tomentosa, L. volutata, Marisa cornuarietis, Melanoides tuberculata* (N), *Mercenaria mercenaria, Parafossarulus manchouricus, Physa acuta* (N), *Physa* sp., *Pila ampullacea* (N), *P. angelica, P. gracilis* (N), *P. polita* (N), *P. scutata* (N), *P. turbinis* (N), *Pisidium abditum, Plesiophysa hubendicki, Pomacea canaliculata* (N), *Segmentina hemisphaerula, Semisulcospira libertine, Sinotaia histrica, S. martensiana* (N), *S. quadrata, Stagnicola elodes, S. emarginata*	Rodents (Humans-aberrant infection)	Cheng and Burton (1965); Richards and Merritt (1967); Alicata and Jindrak (1970); Kocan (1972); Yousif and Lammler (1975*b*); Shiota *et al.* (1980); Arrinda *et al.* (1989); Yen *et al.* (1990); El-Shazly *et al.* (2002); Abo-Madyan *et al.* (2005); Ibrahim (2007); Lv *et al.* (2008)
A. costaricensis	*Biomphalaria glabrata, B. stramina, B. tenagophila, Helisoma trivolvis* (N)	Rodents (Humans-aberrant infection)	Monge *et al.* (1978); Hernan-Camacho and Camacho (1987); Lima *et al.* (1992)
A. dujardini	*Biomphalaria glabrata, Lymnaea corvus, L. peregra, L. stagnalis, Planorbis planorbis*	Rodents	Doby and Drozdz (1971)
A. malaysiensis	*Bellamyia ingallsiana* (N), *Biomphalaria glabrata, Indoplanorbis exustus* (N), *Lymnaea rubiginosa* (N), *Physastra sumatrana, Pila polita, P. scututu* (N)	Rodents	Lim and Ramachandran (1979); Sullivan *et al.* (1978); Lim *et al.* (1977).
A. siamensis	*Biomphalaria glabrata*	Rodents	Kamiya *et al.* (1980)
A. vasorum	*Anisus leucostoma, Biomphalaria glabrata, Lymnaea peregra, L. tomentosa, Physa* sp., *Planorbis planorbis*	Dog, Fox	Guilhon and Gaalon (1969); Eckert and Lammler (1972)
Crenosoma striatum	*Biomphalaria glabrata, Bithynia leachi, Lymnaea peregra, Planorbis* spp.	European hedgehog	Lammler and Saupe (1968); Barus and Blazek (1971)
Cystocaulus ocreatus	*Lymnaea auricularia, L. palustris, L. peregra, L. truncatula, Planorbis* spp.	Sheep, Goat	Kassai (1957), Boev (1975)
Elaphostrongylus panticola	*Lymnaea ovata*	Deer, Elk	Kontrimavichus *et al.* (1976)
E. rangiferi	*Lymnaea auricularia, L. truncatula, L. palustris, L. stagnalis, Planorbarius corneus*	Reindeer	Mitskevich (1964); Skorping (1985)
Filaroides martis	*Gyraulus deflexus, Physa integra*	Mustelids	Anderson (1962)

Muellerius capillaris	*Anisus contortus*, *A. leucostoma*, *A. vortex*, *Gyraulus albus*, *G. laevis*, *Lymnaea auricularia*, *L. corvus*, *L. ovata*, *L. palustris*, *L. peregra* (N), *L. stagnalis*, *L. truncatula* (N), *Omphiscola glabra*, *Physa fontinalis*, *Planorbarius corneus*, *Planorbis planorbis*, *Segmentina nitida*	Sheep, Goat	Kassai (1957); Egorov (1960); Zdzitowiecki (1976)
Neostrongylus linearis	*Lymnaea truncatula*	Sheep, Goat	Hourdin *et al.* (1991)
Oslerus ostratus	*Biomphalaria glabrata*	Cat, Lynx	Wallace and Rosen (1970)
Parelaphostrongylus odocoilei	*Planorbis* sp.	Deer	Brunetti (1969)
P. tenuis	*Lymnaea* sp.	Deer	Anderson (1963*a*)
Protostrongylus rufescens	*Lymnaea peregra*	Sheep, Goat	Urban (1980)
Rauschivingylus asiaticus	*Anisus filiaris*, *Lymnaea* sp., *Valvata sibirica*	Rodents	Domnich (1984)
Syngamus trachea	*Paratenic hosts* *Anisus spirorbis*, *Bithynia tentaculata*, *Lymnaea ovata*, *L. peregra*, *L. stagnalis*, *L. truncatula*, *Planorbarius corneus*, *Valvata piscinalis*	Birds	Barus (1964)
Trilobostrongylus bioccai	*Physa acuta*	Marten	Anderson (1963*b*)
Umingmakstrongylus pallikuukensis	*Aplexa hypnorum*	Muskoxen	Kutz *et al.* (2001)
Varestrongylus alpenae	*Lymnaea reflexa*	Deer	O'Roke and Cheatum (1950)
V. sagittatus	*Lymnaea peregra*, *L. truncatula*, *Planorbarius corneus*	Deer	Rezac (1991)
Order Rhabditida			
Heterohabditis heliothidis	*Oncomelania hupensis*	–	Li *et al.* (1986)
Phasmarhabditis hermaphrodita	*Lymnaea stagnalis*, *Physa fontinalis*	–	Morley and Morritt (2006)
P. tawfiki	*Bellamya unicolor*, *Biomphalaria alexandrina*, *Bulinus truncatus*, *Cleopatra bulimoides*, *Lymnaea caillaudi*	–	Azzam and Tawfik (2003)
Phasmarhabditis sp.	*Bellamya unicolor*, *Biomphalaria alexandrina*, *B. glabrata*, *Bulinus truncatus* (N), *Helisoma duryi*, *Lanistes carinatus*, *Lymnaea cailliaudi*	–	Azzam and Belal (2006)
Pneumonema tiliquae	*Paratenic hosts* *Lymnaea lessoni*, *Physastra* sp.	Lizard	Ballantyne (1991)
Rhabdias americanus	*Paratenic host* *Physa gyrina*	Toad	Langford and Janovy (2009)
Rhabdias eustreptos	*Paratenic host* *Physa gyrina*	Snake	Langford and Janovy (2009)
Rhabdias fuscovenosa	*Paratenic host* *Physa gyrina*	Snake	Langford and Janovy (2009)
Rhabdias joaquinensis	*Paratenic host* *Physa gyrina*	Frog	Langford and Janovy (2009)
Rhabditis sp.	*Biomphalaria alexandrina*	–	Azzam (1998)
Steinernema bibionis	*Oncomelania hupensis*	–	Li *et al.* (1986)
S. carpocapsae	*Oncomelania hupensis*	–	Li *et al.* (1986)
S. glaseri	*Oncomelania hupensis*	–	Li *et al.* (1986)
Order Ascaridia			
Amplicaecum robertsi	*Paratenic host* *Physastra* sp.	Snake	Sprent (1963)

et al. 1990). Generalized responses include an increase in circulating haemocytes immediately following infection, which may be related to the penetration of larvae through the intestinal wall. After a few days levels of these circulating cells decline, probably due to their removal for encapsulation of the parasite. Nevertheless, the haematopoietic organ remains enlarged indicating continued elevated levels of haemocyte production (Noda and Sato, 1990). A further factor determining both focal and generalized responses would appear to correspond to the degree of susceptibility of individual mollusc species. Those species with low susceptibility demonstrate a stronger cellular reaction (Yousif *et al.* 1980).

Rhabditoid infections in aquatic molluscs can cause extensive mortalities (Li *et al.* 1986; Azzam and Tawfik, 2003; Azzam and Belal, 2006; Morley and Morritt, 2006). Nevertheless, no specific details on pathological changes are known. It is likely that they are similar to the effects on terrestrial molluscs. In these hosts the effects of only a limited number of parasites have been elucidated that indicate, in general, that pathology increases with increasing parasite intensity (Morand *et al.* 2004). In addition, infections of *P. hermaphrodita* are known to cause fluid to accumulate in the shell cavity leading to large-scale swelling with both host feeding and activity reduced (Rae *et al.* 2007). The nematodes liberate bacteria on which they feed, from their gut into the host haemolymph where the bacteria multiply rapidly and produce endotoxin. Bacterial septicaemia eventually causes death of the host allowing the nematode to feed and reproduce throughout the cadaver (Rae *et al.* 2007). In contrast, a protein constituent of the haemolymph plasma of *Helix aspersa* inhibited maturation and reproduction, but not growth, of the rhabditoid nematodes *Rhabditis maupasi* and *Steinernema glaseri*. This inhibitory factor may be part of the snail's defence mechanism or simply be a cue utilized by the larvae to synchronise its life cycle with that of its host (Ratanarat-Brockelman, 1975, 1977). The presence of such an inhibitor may be an important factor in the low susceptibility of certain mollusc species to infection.

The cellular response to rhabditoid nematodes by molluscs is poorly understood. Encapsulation of larvae has only been reported in terrestrial species that have a low susceptibility to infection (Rae *et al.* 2008). Interactions with aquatic molluscs remain unknown but are probably similar.

Aquatic molluscs as paratenic hosts

Aquatic molluscs can also act as paratenic hosts for terrestrial nematodes (Table 1) including species that may or may not already utilize snails as intermediate hosts. A paratenic host is one in which the parasite does not undergo any development and may or may not be normally required for transmission to the target host. For nematodes that already utilize molluscs as intermediate hosts the introduction of a further paratenic host can occur because freshwater snails will often feed on the cadavers of dead molluscs (Daldorph and Thomas, 1991). Some nematode larvae can survive and remain viable in decomposing host tissue for many days (Richards and Merritt, 1967) and if the infected cadaver is consumed by scavenging snails then they will ingest and retain the parasite (Rachford, 1975). In contrast, species such as *Syngamus trachea*, *Pneumonema tiliquae* and *Rhabdias* spp. can complete their life cycles directly without the use of an intermediate host but have been experimentally demonstrated to infect aquatic molluscs (Table 1). Studies on *S. trachea* indicate that eggs containing fully developed larvae when deposited into water are ingested by the mollusc and hatch in the digestive tract before penetrating the intestinal wall and locating in the surrounding tissue, with little indication of any host immune response and parasite encapsulation. Snails demonstrate reduced activity after infection but often die when exposed to high parasite numbers. Nematodes retain their viability in the snail host and are infective to the definitive bird host. However, after the death of the mollusc, *S. trachea* larvae did not survive long in the cadaver (Barus, 1964). The role aquatic molluscs may play as paratenic hosts for these species under natural conditions remains to be determined. Nevertheless, it cannot be ruled out that infections of *S. trachea* recorded in wild ducks (Lapage, 1961) may be associated with freshwater snails as they form part of the diet for many waterfowl species.

Emergence and further development of nematodes

Once full nematode development in the snail has been achieved a progression to the next stage of the life cycle becomes a priority. For metastrongyloid nematodes this requires transmission to the definitive vertebrate host that, in many reported cases, occurs by ingestion of the infected mollusc (Anderson, 2000). However, emergence of L3 from snails has been documented in a wide-ranging number of species (Heyneman and Lim, 1967; Boev, 1975; Kontrimavichus *et al.* 1976; Kutz *et al.* 2000). Emergence is not without controversy; with conflicting opinions on the relative ability of certain species to not only achieve it (e.g. Boev, 1975), but also as to its significance as a route of infection (Kralka and Samuel, 1984). Environmental factors, such as rainfall, have been suggested to both trigger and increase the rate of emergence (Boev, 1975; Barcante *et al.* 2003), and may be associated with the degree of stress that changes in these parameters cause to the host snail (Barcante *et al.* 2003). However, in other cases emergence appears to be related to the ongoing development of the L3 stage (Kutz *et al.* 2000). Death of the host can also trigger a large-scale emergence of larval nematodes (Crook *et al*. 1971). Emerged L3 may survive for many days or even months in water, dependent on the species, (Kutz *et al*. 2000; Barcante *et al*. 2003) whilst retaining their infectivity to the target host (Barcante *et al*. 2003).

Transmission of free-living L3 is likely to be achieved under natural aquatic conditions to target hosts through ingestion either whilst drinking from the edge of water bodies or grazing on bank-side flora that has been contaminated with larvae. Nevertheless, infection can also occur through other routes. Larvae can penetrate through abraided skin (Eckert and Lammler, 1972; Ubelaker *et al*. 1981; Wang *et al*. 1991) and, in the case of mice exposed to *A. cantonensis*, successful infections occur through unabraided skin, the footpad, and anal/vaginal/conjunctival mucosa, but not through the thicker skin of the tail (Wang *et al*. 1991). However, it remains unknown whether L3 nematodes can penetrate a vertebrate host in a water medium. Infection may also occur through the ingestion of aquatic paratenic hosts such as fish, frogs and crustaceans that acquire and retain L3 whilst feeding on parasitized molluscs (Anderson, 1962; Wallace and Rosen, 1966, 1967; Ash, 1968; Bolt *et al*. 1993).

In contrast, the emergence of rhabditoid nematodes from aquatic snails is not understood. It is often the case in terrestrial molluscs that, after developing to the L4, they either migrate out of the host to complete their life cycle in the soil or wait for the death of the host to continue development on the cadaver (Morand *et al*. 2004). To facilitate this process nematodes may release symbiotic bacteria whose excreted toxins cause the death of the snail. Mortalities of infected aquatic molluscs occur (Li *et al*. 1986; Azzam and Tawfik, 2003; Azzam and Belal, 2006; Morley and Morritt, 2006) which could be associated with bacterial toxins. Furthermore, in laboratory studies of aquatic snails infected with L4, many hosts have been found dead, attached to the sides of exposure beakers above the water line (Morley and Morritt, 2006). Although the reasons for this are unknown, if such water-leaving behaviour was replicated under natural conditions it would facilitate the transfer of larvae to the bank-side soil allowing completion of their life cycle.

COMPARATIVE SUSCEPTIBILITY OF AQUATIC MOLLUSCS TO TERRESTRIAL NEMATODES

The ability of nematodes to infect molluscs varies from one host species to another and is therefore an important consideration for determining the epidemiology of disease occurrence. Davtjan (1945) was the first to classify molluscs into categories according to their susceptibility to nematode parasites. (1) The obligatory group with the highest prevalences and intensity of infections in which parasite development proceeds more quickly compared to other molluscs under the same conditions. (2) The subobligatory group that has lower prevalences and intensity infections with longer periods of parasite development. (3) The faculative group in which the parasite occurs rarely and, as a rule, develops only with difficulty. (4) The mortal group in which the nematode larvae die after penetration without achieving further developmental stages. (5) The resistant group in which no nematodes are able to infect the host.

Unsurprisingly, given their phylogenetic closeness to land molluscs, aquatic pulmonates are susceptible to a wide range of terrestrial nematodes (Table 1). Prosobranchs, although studied less often, appear almost equally susceptible; however, their operculum may form an effective barrier to infection when they withdraw into the shell. Nevertheless, in general, species from both groups can be classified as being subobligatory in comparison to the susceptibility of terrestrial molluscs, although large variations in prevalence and intensity can occur between species (Yousif and Lammler, 1975*b*; Azzam and Tawfik, 2003). The notable exception to this generalization being *A. cantonensis*-*B. glabrata* where experimental studies have demonstrated a high compatibility between host and parasites comparable with many highly susceptible terrestrial mollusc hosts such as *Achatina fulica*, and this association is therefore likely to be obligatory. However, under field conditions *B. glabrata* has proven to be less susceptible than other freshwater snail species (Azzam and Belal, 2006).

In contrast, infections in bivalve molluscs have only rarely been investigated. It has been established that *Crassostrea virginica*, *C. rizophorne*, *Mercenaria mercenaria*, and *Pisidium abditum* can act as experimental hosts of *Angiostrongylus cantonensis* (Cheng and Burton, 1965; Richards and Merritt, 1967; Arrinda *et al*. 1989) although few third-stage larvae develop (Cheng, 1966). However, in contradiction to these studies, Knapp and Alicata (1967) were unable to experimentally infect both *C. virginica* and *Venerupis philippinarum* with this nematode parasite. Cheng (1967) considered that their negative result was not unexpected with an experimental set-up that impeded 'pumping', an essential part of the oysters feeding mechanism. Infections of *C. virginica* only occur if first-stage larvae of *A. cantonensis* are ingested, and the parasite is able to successfully penetrate the host's intestinal wall (Cheng, 1966). The geographical strain of bivalve used may also be an additional factor in susceptibility (Cheng, 1967). Nevertheless, it is apparent that bivalves are not best suited to be infected by terrestrial nematodes and therefore can only be considered as 'facultative' hosts.

Nevertheless, the compatibility of any particular aquatic mollusc as a host may not be fixed. Susceptibility may be fluid and under continuous parasite exposure may increase. The best examples of this adaptability can be found in studies on trematodes parasitizing pulmonates. When these parasites form a new relationship with an unusual snail host the adaptation of the trematode to the mollusc can occur rapidly due to repeated passage between intermediate and definitive hosts (Boray, 1973). The speed of such adaptation depends on the relative ecological and biological suitability of the particular snail for larval development and the longevity of the parasite in the definitive host (Boray, 1969). In mollusc-nematode associations only limited information of this kind is available. For example, both *B. glabrata* and *Lymnaea palustris* are susceptible aquatic hosts for *A. cantonensis*. However, the percentage of recovered adult parasites from rats was significantly higher following development in *B. glabrata* than in *L. palustris*. Nevertheless, repeated serial passages caused a gradual increase in the number of recovered adult nematodes from those cycled through *L. palustris* until after 4 serial passages the degree of recovered *A. cantonensis* from rats was the same from development in either snail species (Kocan, 1972). Consequently, aquatic molluscs found to be only 'facultative' auxiliary hosts during initial studies may achieve increased compatibility with repeated exposure.

The natural occurrence of parasites within populations may also be profoundly influenced by infra-specific variations in infectivity for either intermediate or definitive host that will shape the ecology of the host-parasite relationship (Webbe, 1971). Nematode parasites of vertebrates demonstrate large geographical variations in infectivity to animal hosts generally regarded as highly susceptible, suggesting that geographical strains are adapted to locally common suitable hosts (Webbe, 1971). Many genetic strains of invertebrate hosts, particularly insects, have also demonstrated variations in susceptibility to nematodes, which may account for many conflicting results of different studies (Webbe, 1971).

Not surprisingly, similar evidence has arisen in studies on mollusc-nematode interactions. For example, an Egyptian and a German strain of *Physa acuta* demonstrated different degrees of susceptibility to *A. cantonensis* in the same study (Yousif and Lammler, 1975*b*), whilst discrepancies between different studies undertaken on infectivity of *E. rangiferi* and *M. capillaris* to *Lymnaea stagnalis* (Skorping, 1982; Zdzitowiecki, 1976) may also be related to host strain. Studies on terrestrial snail susceptibility to *A. cantonensis* have demonstrated that when molluscs from geographical areas where the parasite does not occur are introduced into endemic areas they acquire a lower prevalence of infection, at least initially, than native hosts (Noda *et al.* 1985).

It therefore seems likely that the comparative susceptibility of individual aquatic molluscs to specific terrestrial nematode species may not retain either widespread geographical homogeneity or long-term stability and establishment in any particular aquatic habitat will depend on both the nematode's ability to adapt to new situations, and the favourability of ecological conditions for achieving robust host-parasite associations.

NATURAL NEMATODE INFECTIONS OF AQUATIC MOLLUSCS

It is apparent from these extensive experimental studies that aquatic molluscs may act as hosts for a range of terrestrial nematode parasites. Nevertheless, in the laboratory barriers that may regulate a host-parasite relationship (ecological, geographical and seasonal interactions) are largely removed, facilitating infections in potentially more wide-ranging species.

Studies under natural conditions are therefore of paramount importance to assess the role that aquatic molluscs may play. The transfer of free-living terrestrial nematodes present in the soil into aquatic habitats is relatively straightforward and well documented. Larvae deposited on the soil are mainly disseminated over large distances by water, prior to their contact with a host (Croll, 1975). Storm runoff water will eventually deposit nematodes into a range of both large and small aquatic habitats but particularly into flowing water of streams, rivers and irrigation/drainage canals (Faulkner and Bolander, 1970; Mott and Harrison, 1983). However, there is little tendency for nematodes to settle out in flowing water (Faulkner and Bolander, 1966) and it is only in areas where water velocity is very low, such as in static ponds and lakes as well as sheltered bank-side areas of streams and rivers, that nematodes are likely to accumulate and be a source of infection to aquatic molluscs.

Once contamination of a freshwater habitat occurs the risk of long-term establishment will be dependent on a range of ecological and physiological characteristics of the water body. In particular, the density of susceptible aquatic populations and the frequency of visitation by terrestrial hosts.

Although general surveys of nematode parasites in freshwater molluscs remain rare (Bartlett and Anderson, 1985; Azzam and Belal, 2006), and the occurrence of terrestrial rhabditoids in these snails merely noted (Azzam and Belal, 2006), a limited number of field studies on specific metastrongyloid species in aquatic hosts have been undertaken (Table 1). In particular, because of the widespread human consumption of raw or partially cooked freshwater snails in endemic areas, the medically important metastrongyloid *A. cantonensis* has been extensively studied concurrently in both terrestrial and freshwater habitats.

In general, *A. cantonensis* is a tropical species but has been found in both the colder climate of northern Japan (Ishii, 1984) and at the edge of the Sahara desert in the Egyptian Nile basin (Yousif and Ibrahim, 1978; El-Shazly *et al.* 2002; Ibrahim, 2007). Transmission is favoured in the majority of sites through terrestrial molluscs, particularly the giant African land snail, *Achatina fulica* (Alicata and Jindrak, 1970). However, in certain habitats where more extreme environmental conditions prevail, such as the flooded rice fields of South-East Asia and the Egyptian waterways, aquatic molluscs take a more prominent role.

Surveys have shown that infected freshwater snails are only recovered on the edges of water bodies (Tesana *et al.* 2009) where the ecotone between terrestrial and aquatic hosts occurs. Prevalence of infections can fluctuate from one aquatic habitat to another, probably associated with the density of potential hosts and the ecology of individual water bodies (Tesana *et al.* 2009). Indeed, the related species *A. malaysiensis* has a higher prevalence in freshwater snails sampled from static water sites (rice-fields and ponds) than flowing water sites (streams) (Lim and Ramachaudran, 1979). Increasing levels of salinity cause a reduction in the occurrence of *A. cantonensis* infections (Ibrahim, 2007). Although L1 have been experimentally demonstrated to tolerate high salinity levels they have a reduced activity (Richards and Merritt, 1967), this may impair their ability to infect aquatic molluscan hosts under these conditions.

The occurrence of terrestrial nematodes in aquatic molluscs may change temporally as well as spatially. Seasonal variations in *A. cantonensis* prevalence occur in aquatic molluscs with greater prevalence during the 'dry' compared to 'rainy' season in the tropics (Yen *et al.* 1990), possibly due to heavy rainfall diluting the number of larvae in the irrigation canals sampled, and the increasing water flow reducing transmission opportunities (Yen *et al.* 1990). Similarly in Egypt, prevalences were highest in spring and summer when aquatic molluscs were most active (Ibrahim, 2007). Periodic disturbance of the habitat can also affect infection levels in freshwater snails. *Angiostrongylus malaysiensis* has higher prevalences in aquatic molluscs sampled from rice-fields used continuously than in those fields allowed to dry out for several months after crop harvesting (Liat *et al.* 1977). The drying out of temporary water bodies such as rice-fields may interfere with the interactions between aquatic and terrestrial host-parasite systems at a local level. Nevertheless, definitive rodent hosts can simply switch to feeding on aquatic molluscs at nearby fields that remain flooded, ensuring that transmission dynamics are unaffected at a regional scale.

It is likely that the risk of aquatic mollusc acquiring infections will vary from one terrestrial nematode species to another. For rhabditoids infecting terrestrial molluscs the chance of transfer into aquatic habitats is high. Many species of both land snails and slugs have a high affinity for moist soil conditions and can often be found in relatively high densities close to freshwater habitats (Boycott, 1934; Horsak and Cernohorsky, 2008). Such a close association provides a relatively straightforward route for the transfer of nematode larvae, whether in the soil or within terrestrial mollusc cadavers, into the water medium during periods of rainfall.

In contrast, for metastrongyloids the relationship the definitive vertebrate host has with open bodies of water will be a key factor in determining infection levels in freshwater snails. For example, infections of *M. capillaris* from aquatic sources to sheep and goats are considered to take place mainly when these animals are drinking from shallow water bodies. However, because they drink only a few times during the day and the act of drinking is itself relatively brief they have only a transient relationship with water, and consequently the transmission window for these nematodes to both infect and emerge from freshwater snails is limited (Egorov, 1960). Such a narrow window of opportunity may be a factor, in conjunction with geographical variations in susceptibility, for the conflicting results of field studies on *M. capillaris* infections in freshwater molluscs. Trushin (1976) examined almost 14 000 aquatic snails but found none infected in Tver province, northwest of Moscow. In contrast, Egorov (1960) found 0·3% of freshwater molluscs infected, which compared favourably with the 1·07% of terrestrial snails and 5·2% of slugs infected in the same endemic *M. capillaris* area near St Petersburg, Russia.

However, other definitive hosts, such as rodents infected with *A. cantonensis*, are often found associated with aquatic habitats feeding on freshwater molluscs and other potential paratenic animal hosts (Yousif and Ibrahim, 1978), facilitating a smoother cycling between terrestrial and aquatic environments. This is reflected in the widespread occurrence of *A. cantonensis* in freshwater molluscs at these localities (Ibrahim, 2007; Tesana *et al.* 2009). Indeed, in the related species, *A. malaysiensis*, variations in the worm-burden of four species of rat sampled from the vicinity of aquatic habitats were not due to differences in their susceptibility but rather were associated with local habitat preference and fluctuations in prevalence and intensity within molluscan hosts found there (Liat *et al.* 1977). Mustelids, such as mink, also have strong affinities with water bodies, readily feeding on fish and frogs that may act as paratenic hosts for species such as *Aelurostrongylus pridhami* and *Filaroides martis*, increasing the likelihood of aquatic molluscs acting as intermediate hosts (Anderson, 1962).

However, natural transmission of metastrongyloids to vertebrate hosts via the aquatic medium is difficult to prove conclusively. In particular, infections from drinking water contaminated with L3 appear almost impossible to determine in any individual case or large outbreak (Rosen *et al.* 1967). Nevertheless, sources of human infections of *A. cantonensis* can be sufficiently narrowed down through patient interviews to a few probable routes of exposure. These findings suggest that in a number of cases transmission occurred through ingestion of infected aquatic molluscs, crustaceans, frogs, fish, or bankside fruit contaminated with L3 (Witoonpanich *et al.* 1991; Brown *et al.* 1996; Thobois *et al.* 1996; Lai *et al.* 2007; Malvy *et al.* 2008). It seems logical to assume that wildlife infections may also be acquired in a similar manner.

AQUATIC MOLLUSCS AS HOSTS IN A CHANGING CLIMATE

Global climate change resulting from anthropogenic activities is now a widely accepted phenomenon. Alterations in temperature, rainfall patterns and soil humidity are likely to occur on a global, regional, and local scale causing changes in average values and an increase in the frequency of extreme events such as flooding and droughts (Morand and Guegan, 2008). A large range of important factors that structure complex host-parasite systems may alter under the pressure of climate change (Hoberg *et al.* 2008). These alterations may be numerical (density, prevalence, and abundance changes in both hosts and parasites), functional (altered ecological structure, geographical distribution, phenology or host associations), or micro-evolutionary through local adaptation (Hoberg *et al.* 2008). Although changes in host-parasite dynamics will likely fluctuate between geographical localities and the individual requirements of each species interactions, it is probable that climate change will influence helminths most strongly in temperate and colder latitudes where modifications of climatic variables are more pronounced (Mas-Coma *et al.* 2008). Evidence for this is already emerging in a nematode-mollusc-ungulate system within the Arctic (Kutz *et al.* 2005; Jenkins *et al.* 2006) because the transmission of parasites through terrestrial molluscs is particularly susceptible to fluctuating climatic conditions (Georgiev *et al.* 2003; Jenkins *et al.* 2006; Morley and Lewis, 2008). Extreme changes in climate can therefore have profound effects on these host-parasite relationships. The resulting ecological perturbations will alter the dynamics of parasite transmission, increasing the potential for host switching and facilitating new host-parasite associations (Brooks and Hoberg, 2007). It therefore seems logical to assume that mollusc-nematode interactions will be particularly susceptible to both large and small scale shifts in the spectrum of hosts utilized and the pressure of extreme climatic events may lead to a greater role for aquatic snails.

Changes in temperature, rainfall and vegetation could modify transmission through the molluscan host causing changes in geographical distribution, density and survival of both parasite and snail (Mas-Coma *et al.* 2008). For example, an increase in average temperatures has the obvious effect of accelerating development of nematodes within the mollusc. This may be particularly important in high latitudes where cycling of the parasite may be accomplished in a single summer rather than over multiple years (Kutz *et al.* 2005). At temperate latitudes it may facilitate cycling to occur numerous times over the course of a year whilst the geographical range of certain species may expand e.g. *A. vasorum* (Morgan *et al.* 2009).

Rainfall is a particular key factor in defining the scope of aquatic molluscs' involvement in terrestrial nematode transmission. Increased occurrence of heavy, persistent rainfall provides more and improved aquatic habitats for snail development, whilst at the same time escalates the risk of widespread flooding. This can be particularly devastating to terrestrial molluscs causing 'over-hydration' in exposed communities resulting in high mortalities from drowning (Peake, 1978), and in protractedly wet environments population densities can often be reduced (Peake, 1978; Plum, 2005) whilst new species of aquatic molluscs may appear (Plum, 2005). Storm and flood runoff water will deposit cadavers of drowned infected terrestrial molluscs into both still and flowing water environments (Wallace and Rosen, 1967) where they can form a source of infection for a range of paratenic aquatic hosts, including molluscs, crustaceans, frogs and fish, that scavenge on the carcasses. Mature L3 may also emerge from drowned terrestrial molluscs in the freshly contaminated body of water increasing the risk of infecting wildlife that may frequent it. Flooding will also cause an increased frequency in the transfer of free-living nematode stages into aquatic habitats. Under such circumstances aquatic molluscs will naturally acquire infections and play a greater role in the transmission of many parasites. This scenario has been elegantly demonstrated by field studies on the occurrence of *Angiostrongylus* spp. within the flooded rice-fields and waterways of South-East Asia (Liat *et al.* 1977; Lim and Ramachandran, 1979; Tesana *et al.* 2009).

At the other end of climatic extremes drought, especially during the summer when it may be accompanied by a heat wave, can also have devastating effects on parasite transmission. Terrestrial molluscs, under such conditions, spend prolonged periods aestivating, reducing the likelihood of contact with free-living parasite stages (Morley and Lewis, 2008). Under such constraints nematodes may have to spend extensive periods in the environment exposed to adverse climatic conditions. Survival in direct sunlight may be impaired by the heat generated in or on the soil, by the increased risk of desiccation, and by the pathological effects of elevated ultraviolet light levels (Kates, 1965; Gaugler and Boush, 1978; van Dijk *et al.* 2009). Consequently under arid or semi-arid conditions only 'minimal transmission' will normally occur (Kates, 1965), infections being maintained by small areas where soil moisture and some shade are provided (Kates, 1965; Glazer *et al.* 1991). Bank-side areas with overhanging vegetation of both small and large water bodies provide the conditions necessary to maintain 'minimal transmission' under such adverse climate and are likely to prove attractive to many potential terrestrial hosts. With increased contact with water comes a more likely chance of aquatic molluscs becoming infected as these hosts do not need to aestivate to the same extent as their terrestrial counterparts, and elevated numbers of nematodes will be deposited in the soil within the wash zone of the aquatic habitat. Again the occurrence of *A. cantonensis* in the desert environment of the Egyptian Nile basin (El-Shazley *et al.* 2002; Ibrahim, 2007) provides an elegant model for nematode transmission under these conditions.

Nevertheless, climate does not act gradually or entirely predictably on ecosystems. Instead, in combination with other influences, such as geographical variables, it produces threshold effects on populations inducing changes in infectious disease dynamics (IOM, 2008). The nature of host utilization by nematodes is therefore likely to be influenced either directly or indirectly by local, regional, or global variations in a range of factors, that are nevertheless closely interrelated and influenced by climate, but may produce variable pressure on nematode transmission dynamics and consequently result in fluctuating utilization of aquatic molluscs as hosts.

CONCLUDING REMARKS

It is apparent from this study that much of what is known on terrestrial nematodes parasitizing aquatic molluscs arises from species that are of veterinary, medical, or commercial interest. Such a selection will tend to limit the extent of our understanding and therefore more basic research is necessary, particularly for rhabditoids of which almost nothing is known about their natural occurrences in aquatic molluscs.

Nevertheless, it seems likely that, geographically, infections of aquatic molluscs most likely occur adjacent to those terrestrial habitats associated with a relatively high nematode density and where the ecotone between land and water is particularly broad and continuous.

That aquatic molluscs are the dominant hosts for *A. cantonensis* in both arid and flooded environments is particularly striking and suggests that the environmental conditions in a habitat play a key role in structuring the intermediate host fauna utilized by nematodes. As the impact of climate change becomes increasingly apparent, the deterioration of standard host-parasite associations is increasingly likely as traditional habitats decline in transmission viability. Under such extreme environments the role of aquatic molluscs in transmitting terrestrial nematodes may therefore become increasingly prominent.

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