Review of experimental and natural invertebrate hosts of sealworm (*Pseudoterranova decipiens*) and its distribution and abundance in macroinvertebrates in eastern Canada

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ABSTRACT

Experimental and natural invertebrate intermediate hosts of sealworm (*Pseudoterranova decipiens*) as well as transmission experiments of sealworm from invertebrates to fish are reviewed and summarized. Experimental hosts include copepods, mysids, cumaceans, isopods, amphipods, decapods, annelids, and molluscs. Invertebrates collected from eastern Canada between 1989 and 1995 were checked for nematode infections by microscopic examination of dissected animals or enzymatic digestion of bulk samples. Third-stage larval sealworm were found in mysids (*Neomysis americana*, *Mysis stenolepis*) from Passamaquoddy Bay, the Bras d'Or Lakes, inshore Cape Breton, Sable Island and Sable Island Bank. Infected amphipods (*Amphiporeia virginiana*, *Americorchestia megalophthalma*, *Gammarus* spp.) were found only on Sable Island. Typical infection rates in macroinvertebrates were 1-4/1000. No sealworm infections were found in approximately 18,000 amphipods examined from Sable Island Bank, the site of the most heavily infected fishes in eastern Canada. In Wallace Lake, a brackish pond on Sable Island, infection rates were much higher in mysids than in amphipods. Estimates of rates of transmission of sealworm from invertebrates to fish were derived from infection levels in Wallace Lake and feeding experiments involving sticklebacks and invertebrate prey. It is concluded that mysids may be much more important than amphipods in transmitting sealworm to fish hosts.

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INTRODUCTION

Sealworms (*Pseudoterranova decipiens*) are parasitic nematodes (Anisakidae) whose adults infect stomachs of seals. Eggs are passed with the feces and sink to the bottom at a rate of 1.01 x 10^{-4} m/s (McConnell *et al*. 1997), where free-living larvae hatch. There is debate over how many moults occur in the egg, and whether an L_2 or an L_3 stage larva hatches (Koie *et al*. 1995, Measures and Hong 1995). Development and hatching are temperature, but not salinity, dependent (Brattey 1990, Measures 1996). These larvae are infective to invertebrates, which transmit the larvae to fish when ingested (McClelland *et al*. 1983). Seals typically acquire the parasite by ingesting infected fish.

Three sibling species designated *Pseudoterranova decipiens* A, B and C have been found in the North Atlantic, with types B and C occurring in Canadian waters (Paggi *et al*. 1991). Type B (*P. decipiens* sensu stricto after Paggi *et* *al*. 2000) is found primarily in grey seals (*Halichoerus grypus*), but also in harbour seals (*Phoca vitulina*) in the western North Atlantic, and type C is found only in bearded seals (*Erignathus barbatus*) (Paggi *et al*. 1991). Bristow and Berland (1992) suggested that the data on sealworm distribution and abundance from the Gulf of St. Lawrence must be interpreted carefully because all three seal species are found there. However, this is incorrect as the bearded seal occurs rarely in the Gulf, being confined to colder waters off Labrador and to the north. All sealworms recovered from seals and fish off Nova Scotia, Newfoundland, and the Gulf of St. Lawrence are *P. decipiens* B (Paggi *et al*. 1991, Brattey and Davidson 1996, Brattey and Stenson 1993). Thus, surveys of invertebrates, fish and seals in the regions of eastern Canada discussed herein are dealing with only one species of sealworm. In European waters, the situation is more complex, with considerable geographic overlap of sibling species A and B (Paggi *et al*. 1991).

A variety of microcrustaceans and macroinvertebrates have been infected experimentally with the sealworm (McClelland 1982, McClelland 1990). Nonetheless, until recently, records of natural infections of sealworm in invertebrates were sporadic and important questions pertaining to sealworm transmission remained unanswered. Herein, experimental and natural infections of sealworm in invertebrates are reviewed and integrated together with new developments in understanding the sealworm life cycle.

EXPERIMENTAL RECORDS

McClelland (1982) successfully infected 12 species of harpacticoid copepods and one cyclopoid with larvae hatched from eggs obtained from gravid female sealworms recovered from harbour and grey seals (Table 1). The success rate of experimental infections varied from 58% to 100% in prevalence and 1.25 to 18.10 in mean intensity among the species and stages tested. Mature females developed the heaviest infections. Calanoid copepods (*Eurytemora* sp. and *Pseudocalanus* sp.) did not become infected, though one unpublished record of an infected calanoid exists (see Burt in McClelland 1995). Larvae in infected copepods demonstrated considerable growth, but little morphological change and no moult was detected (McClelland 1982).

A variety of macroinvertebrates have been infected experimentally with sealworm. These include five species of decapods, three species of amphipods, and single species of polychaete, nudibranch, mysid, cumacean, and isopod (Table 1) (Jarecka *et al*. 1988, McClelland 1990, Burt 1994). Among these hosts, the cumaceans, isopods and decapods displayed a haemocytic response which destroyed the parasite (McClelland 1990). The amphipods *Gammarus oceanicus*, *Gammarus lawrencianus* and *Unciola irrorata* and crab zoea could be infected upon direct exposure to newly-hatched larvae (Jarecka *et al*. 1988, McClelland 1990). However, serial transmissions involving benthic copepods (*Halectinosoma*, *Tisbe*, *Ameira* and *Paracyclopina* spp.) as initial hosts proved much more efficacious (McClelland 1990). All other macroinvertebrates only became infected upon exposure to infected copepods, but not to newly-hatched larvae (McClelland 1990). McClelland (1990) used adult gravid female sealworms from grey seals as a source of infective larvae in his experiments, whereas Jarecka *et al*. (1988) used worms from both grey and harbour seals with varying success. Burt (1994) infected *G. oceanicus* with hatched larvae produced by worms from grey seals, but was unable to obtain infections with those from harbour seals.

Sealworms did not survive beyond 21 days after free-living larvae were intraperitoneally injected or administered orally into rainbow trout (*Oncorhynchus mykiss*) (Smith *et al*. 1990), implying that invertebrate intermediate hosts are a requirement for completion of the sealworm life cycle. In a further set of experiments, McClelland (1995) demonstrated that only worms larger than 1.41 mm in length, and usually larger than 2.00 mm, were infective to fish. As sealworms cannot attain this size in microinvertebrate hosts such as copepods, these results imply that macroinvertebrates are an essential component of transmission. However, efficiency of transmission improves when a microcrustacean host is incorporated into the life cycle (McClelland 1995).

Table 1. List of invertebrates experimentally infected with the sealworm (*Pseudoterranova decipiens*). Direct transmission refers to exposing the invertebrate to the free-living infective larvae. Serial transmission refers to exposing the invertebrate to an infected precursor invertebrate host, such as a copepod.

Species	Mode of transmission	Reference
Crustacea		
Copepoda (Harpacticoida)		
Halectinosoma spp.	direct	McClelland (1982)
Danielsennia typica	direct	McClelland (1982)
Tisbe furcata	direct	McClelland (1982)
Tisbe spp.	direct	McClelland (1982)
Alteutha sp.	direct	McClelland (1982)
Diosaccidae g. sp.	direct	McClelland (1982)
Ameira longipes	direct	McClelland (1982)
Enhydrosoma carticauda	direct	McClelland (1982)
Phyllothallestris sp.	direct	McClelland (1982)
Tachidius brevicornis	direct	Jarecka *et al*. (1988)
Macrostella sp.	direct	Jarecka *et al*. (1988)
Parathalestris sp.	direct	Jarecka *et al*. (1988)
Copepoda (Cyclopoida)		
Paracyclopina sp.	direct	McClelland (1982)
Copepoda (Calanoida)		
Tortanus discaudata	direct	Burt (in McClelland 1995)
Mysidacea		
Mysis stenolepis	serial	McClelland (1990)
Cumacea		
Diastylis polita	serial	McClelland (1990)
Isopoda		
Edotea triloba	serial	McClelland (1990)
Amphipoda		
Gammarus lawrencianus	direct	Jarecka *et al*. (1988)
Gammarus oceanicus	direct, serial	McClelland (1990)
Unciola irrorata	direct, serial	McClelland (1990)
Decapoda		
Crangon septemspinosa	serial	McClelland (1990)
Palaemontes vulgaris	serial	McClelland (1990)
Hyas coarctatus zoea	direct	Jarecka *et al*. (1988); Burt (1994)
Hyas araneus zoea	direct	Jarecka *et al*. (1988); Burt (1994)
Cancer borrealis zoea	direct	Jarecka *et al*. (1988); Burt (1994)
Annelida (Polychaeta)		
Phyllodoce sp.	serial	McClelland (1990)
Mollusca (Nudibranchia)		
Coryphilla sp.	serial	McClelland (1990)

NATURAL INFECTIONS

Naturally infected invertebrates have been found in both Canadian and European waters (Fig. 1). These include mysids and gammarid amphipods in eastern Canada (Scott and Black 1960, McClelland 1990, Marcogliese 1992a, 1993a, 1993b, 1996a, Marcogliese and Burt 1993, Jackson *et al*. 1997), and gammarid and caprellid amphipods, prawns, mysids, and polychaetes in Europe (Uspenskaya 1960, Val'ter and Popova 1974, Val'ter 1978, 1987, Lick 1991) (Table 2). In addition, infected isopods and mysids have been found in the stomach contents of Atlantic cod (*Gadus morhua*) in Norway and American plaice (*Hippoglossoides platessoides*) from Sable Island Bank respectively (Bjorge 1979, Martell and McClelland 1995). However, until recently, little quantitative data on infections were available. No records of invertebrates infected with sealworm are available from the Pacific Ocean or the southern hemisphere.

Normally, determination of infection in invertebrates requires dissection and microscopic examination of individuals (Fig. 2), a very time-consuming and laborious process, perhaps

Fig. 1. *A variety of methods are used to sample invertebrates for parasite analysis, including dip nets, traps and benthic sleds. Photo: D. Marcogliese*

explaining the paucity of data. Using a modified Baermann apparatus (Marcogliese 1992a, 1993a, 1993b, 1996a, Marcogliese and Burt 1993, Jackson *et al*. 1997), large numbers of invertebrates can be processed fresh to obtain live nematodes, a technique permitting proper fixation of parasites for morphometric study. The drawback of this system is that only total number of worms in the sample may be determined, but multiple infections per host can not. Thus, mean abundance (mean number of parasites per animal) can be determined correctly, but not necessarily prevalence (percentage of animals infected). However, abundances are usually so low in invertebrate intermediate hosts that multiple infections are extremely rare (though a single mysid containing two sealworms was found by microscopic examination from Wallace Lake, Sable Island, in 1994). Rates of infection in the natural environment tend to be in the order of 0.2-7.5 sealworms per 1000 invertebrates (Table 3). Generally, when quantita-

Table 2. List of invertebrates found naturally infected with sealworm (*Pseudoterranova decipiens*).

Species	Location	Reference
Crustacea		
Mysidacea		
Mysis mixta	Bras d'Or Lakes, N.S.	Scott and Black (1960)
	Sable Island Bank, N.S.[2]	Martell and McClelland (1995)
Mysis stenolepis	Bras d'Or Lakes, N.S.	Scott and Black (1960)
	Brandy Cove, Passamaquoddy Bay, N.B.	Marcogliese and Burt (1993)
Neomysis integer	Elbe estuary	Lick (1991)
Neomysis americana	Wallace Lake, Sable Island, N.S.	Marcogliese (1992a, 1993a, 1996a)
	Sable Island Bank, N.S.	Marcogliese (1996a)
Mysis stenolepis +/or	Bras d"Or Lakes, N.S.	Jackson *et al*. (1997)
Neomysis americana	St. Ann's Bay, Cape Breton Island, N.S.	Jackson *et al*. (1997)
Isopoda		
Idothea neglecta[2]	Norway	Bjorge (1979)
Amphipoda (Gammaridea)		
Marinogammarus obtusatus	White Sea	Val'ter (1987)
Gammarus lawrencianus	Northwest Arm, N.S.	McClelland (1990)
Unciola irrorata	Northwest Arm, N.S.	McClelland (1990)
Americochestia megalophthalma	North beach, Sable Island, N.S.	Marcogliese (1993a)
Amphiporeia virginiana	South beach, Sable Island, N.S.	Marcogliese (1993b)
Gammarus spp.[1]	Wallace Lake, Sable Island, N.S.	Marcogliese (1996a)
Amphipoda (Caprellidea)		
Caprella septentrionalis	White Sea	Val'ter (1978)
Decapoda		
Sclerocrangon boreas	Barents Sea	Uspenskaya (1960, 1963)
Annelida (Polychaeta)		
Lepidonotus squamatus	White Sea	Val'ter and Popova (1974)

[1] Amphipods were reported as *Gammarus oceanicus* in Marcogliese (1992) and *G. oceanicus* and *Gammarus setosus* in Marcogliese (1993a). However, there since has been some disagreement between experts who have examined the specimens of *G. setosus*, one claiming it is *G. setosus* and another, *G. lawrencianus*. For that reason they were reported as *Gammarus* spp. in Marcogliese (1996a), and that nomenclature is retained herein.

[2] These infected host specimens were collected from the stomach contents of fish.

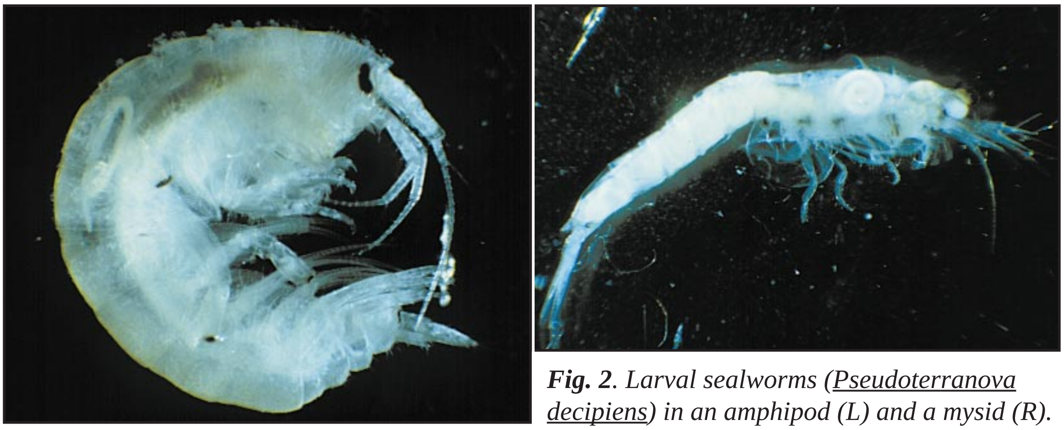

***Fig. 2**. Larval sealworms (Pseudoterranova decipiens) in an amphipod (L) and a mysid (R). Photo: D. Marcogliese*

tive data are available, they suggest that mysids are more important than amphipods as intermediate hosts of sealworm in eastern Canada. Naturally infected amphipods were found only on Sable Island (Marcogliese 1993a, 1993b, 1996a), the home of the largest breeding colony of grey seals in the Northwest Atlantic, and in the Northwest Arm, near Halifax, Nova Scotia (McClelland 1990). The finding of infected invertebrates in the Northwest Arm is puzzling because there is no seal population in that vicinity. In contrast, infected mysids were found in or on Sable Island, Sable Island Bank, Passamaquoddy Bay, St. Ann's Bay and the Bras d'Or Lakes (Fig. 3). When amphipods and mysids were collected from the same site, mean abundance in mysids was higher than in amphipods (Marcogliese 1992a, 1993a, 1996a).

Table 3. Mean abundance of sealworm (*Pseudoterranova decipiens*) reported in quantitative surveys of invertebrates (expressed as number of sealworms per 1000 invertebrates).

Host	Location	Abundance	Reference
Mysis spp.	Bras d'Or Lakes (1958)	0.6	Scott and Black (1960)
Lepidonotus squamatus	White Sea (1962-67)	1.0	Val'ter and Popova (1974)
Marinogammarus obtusatus	White Sea (1984)	7.5	Val'ter (1987)
Gammarus lawrencianus	Northwest Arm	1.5	McClelland (1990)
Unciola irrorata	Northwest Arm	2.0	McClelland (1990)
Neomysis americana	Wallace Lake (1990)	1.1	Marcogliese (1992a)
Neomysis americana	Middle Wallace Lake (1995)	1.5	Marcogliese (1992a)
Neomysis americana	Wallace Lake (1991)	0.9	Marcogliese (1993a)
Neomysis americana	Wallace Lake (1994)	4.0	Marcogliese (1996a)
Neomysis americana	Sable Island Bank (1995)	2.3	Marcogliese (1996a)
Mysis stenolepis	Brandy Cove (1991)	2.0	Marcogliese and Burt (1993)
Mysis stenolepis + *Neomysis americana*	Bras d'Or Lakes (1993)	0.2	Jackson *et al*. (1997)
Mysis stenolepis + *Neomysis americana*	St. Ann's Bay (1993)	0.5	Jackson *et al*. (1997)
Americochestia megalophthalma	North beach, Sable Is. (1990)	4.6	Marcogliese (1993a)
Americochestia megalophthalma	North beach, Sable Is. (1991)	1.3	Marcogliese (1993a)
Amphiporeia virginiana	South beach, Sable Is. (1991)	2.5	Marcogliese (1993b)
Amphiporeia virginiana	South beach, Sable Is. (1992)	1.0	Marcogliese (1993b)
Gammarus spp.	Wallace Lake (1992)	0.5	Marcogliese (1996a)
Gammarus spp.	Wallace Lake (1994)	0.3	Marcogliese (1996a)

Fig. 3. *Map of eastern Canada showing locations where macroinvertebrates naturally infected with sealworm (Pseudoterranova decipiens) have been found. Sites are: 1) Passamaquoddy Bay; 2) Northwest Arm; 3) Sable Island; 4) Sable Island Bank; 5) Bras d'Or Lakes; and 6) St. Ann's Bay.*

NEGATIVE RECORDS

Though polychaetes have been implicated in the sealworm life cycle, no sealworm were found from 4,819 polychaetes collected from Sable Island Bank in 1989-90 (Marcogliese 1996b). Nor were sealworms found in 17,800 amphipods belonging to 36 species from Sable Island Bank and vicinity, including 3,874 specimens of *Unciola irrorata*; 1,254 mud shrimp (*Crangon septemspinosa*); 780 hermit crabs (*Pagurus* spp.); 1,147 cumaceans; 735 isopods; or 170 megalops of *Cancer irrorata* (Marcogliese 1993a, 1996b, Jackson *et al*. 1997). Most of these specimens were collected from areas close to Sable Island, the waters around which contain the highest levels of infection in fish in eastern Canada (McClelland *et al*. 1985, 1987). Infected mysids (*Neomysis americana*), however, were collected from the same locality (Marcogliese 1996a). Nor were sealworms found in 3,500 amphipods from Passamaquoddy Bay, New Brunswick, including 1,047 specimens of *Marinogammarus obtusatus* and 1,664 of *Caprella linearis*, though one infected mysid (*Mysis stenolepis*) was found (Marcogliese and Burt 1993, Marcogliese 1996b). The two latter amphipods were collected either directly on or near harbour seal haul-out sites. In addition, no sealworm were found in 1,360 *Gammarus lawrencianus* and *Gammarus oceanicus* collected in Metis Bay, in the St. Lawrence estuary (Jackson *et al*. 1997). No sealworm were found from over 800 crab zoea and 294 isopods (*Idotea balthica*) collected in the Bras d'Or Lakes, where infected mysids also were found (Jackson *et al*. 1997). In addition, 405 specimens of *I. balthica* from Prince Edward Island, an area of high sealworm abundance in fish, were not infected (Jackson *et al*. 1997).

Many of the organisms mentioned in the preceding paragraph or closely related species have previously been recorded as natural or experimental hosts for sealworm (Val'ter 1978, 1987, Bjorge 1979, McClelland 1990) (See Tables 1 and 2). Among amphipods, *M. obtusatus* and a caprellid, *Caprella septentrionalis*, were infected in the White Sea (Val'ter, 1978, 1987), and *G. lawrencianus* and *U. irrorata*, in the Northwest Arm, Nova Scotia (McClelland 1990). The isopod *Idotea neglecta* was found among fish stomach contents (Bjorge 1979). Successful laboratory infections include *G. lawrencianus*, *G. oceanicus*, *U. irrorata*, *C. septemspinosa* and crab zoea (Jarecka *et al*. 1988, McClelland 1990, Burt 1994). Yet, negative results may be biased due to limited sample sizes and other confounding factors. However, when comparative quantitative data are available, as from various sites in eastern Canada, mysids typically are infected with sealworm while other potential hosts often are not, the only exception being samples directly on Sable Island. These results further imply that mysids are more important than other organisms in sealworm transmission.

TRANSMISSION TO FISH

On Sable Island Bank, a comparative quantitative survey of three sympatric pleuronectids with varying degrees of sealworm abundance demonstrated a strong association of sealworm infection with the amount of suprabenthic prey, and to a lesser extent epibenthic prey, in the diet (Martell and McClelland 1995). American plaice had the heaviest infections, followed by yellowtail flounder (*Pleuronectes ferrugineus*) and lastly, winter flounder (*Pleuronectes americanus*). American plaice principally consume cumaceans, amphipods, mysids, and pagurids; yellowtail flounder primarily polychaetes, cumaceans, amphipods, and tunicates; and winter flounder mainly polychaetes, crustaceans, and tunicates (Martell and McClelland 1994).

Length of sealworms from naturally infected macroinvertebrates varies from 1.1 to 9.0 mm (McClelland 1990, Marcogliese 1992a, 1993a, 1993b, Marcogliese and Burt 1993, Jackson 1995, Martell and McClelland 1995). McClelland (1995) demonstrated that a minimal size of sealworm larvae must be attained in the invertebrate host to allow successful transmission to fish. However, in his experiments larger fish tended to be refractory to infection via infected invertebrates, leading him to propose that the small larvae in invertebrates may have difficulty in establishing in larger fish because of the extensive migration required. Moreover, small nematodes are rarely found in naturally infected commercial fishes, but do occur in experimentally-infected and wild-caught small benthophagous fishes (McClelland 1995). By implication, these small fishes may be important as bridges between macroinvertebrates and large piscivorous fish (McClelland and Martell 2001).

The discovery of infected populations of threespine (*Gasterosteus aculeatus*) and fourspine (*Apeltes quadracus*) sticklebacks in brackish ponds frequented by harbour seals on Sable Island (Marcogliese 1992b) permitted examination of the sealworm life cycle and transmission dynamics in an enclosed relatively simple ecosystem consisting of few invertebrate and fish species (Marcogliese 1996a). Mysids (*Neomysis americana*) were more heavily infected than amphipods (*Gammarus* spp.), their infec tion levels being positively correlated with those in fourspine sticklebacks. Both threespine and fourspine sticklebacks fed preferentially on mysids over amphipods. Given the infection rates of *N. americana* and *Gammarus* spp. and their respective densities in Wallace Lake, densities of infected invertebrates could be calculated. The density of infected mysids (1.5 per m^2) was greater than that of infected amphipods (0.36 per m^2) in the pond. These results imply that the probability of a fish encountering an infected mysid is greater than that of an infected amphipod, despite the fact that amphipods were almost three times as numerous as mysids. By integrating the data on infection levels in invertebrates with information derived from feeding experiments, the rate of transmission of sealworm from invertebrates to fish could be determined. Transmission rate was about 100 times higher via mysids than via amphipods, and fish accumulated parasites at a rate of about 1 per month from mysids. These rates may be similar to those experienced by small benthophagous fish at sea, given that infection densities in Wallace Lake sticklebacks are similar to those of certain small benthophagous fishes on the Scotian Shelf (McClelland 1995), that mysids are preferred prey, and that infection levels are comparable between mysids from Wallace Lake and Sable Island Bank (Table 3).

Distribution records of sealworm in invertebrate hosts from eastern Canada, both from areas of high sealworm abundance in fish and from Wallace Lake, Sable Island, suggest mysids are extremely important intermediate hosts of *P. decipiens*. Indeed, mysids are probably more important than amphipods in transmission of sealworm to fish, but the role of amphipods in the transmission process should neither be ignored nor underestimated.

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