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FIRST RECORD OF PARATENIC HOSTS OF THE SWIMBLADDER NEMATODE *ANGUILLICOLA CRASSUS* IN NORTH AMERICA

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ABSTRACT: *Anguillicola crassus* is a non-native parasite of the American eel, *Anguilla rostrata*. Since being introduced into North America, the nematode has spread rapidly across the range of *A. rostrata*, but paratenic hosts, which may facilitate parasite dispersion, have yet to be identified in the region. We investigated infection of larval *A. crassus* in 261 fish specimens belonging to 23 species and 12 orders collected from estuarine habitats in South Carolina (salinities 0–9 ppt) and Nova Scotia (10–18 ppt). A total of 35 fish belonging to 5 species and 3 orders were infected with the third-stage larvae (L_3) of *A. crassus*, providing the first record of paratenic hosts for the parasite in North America. In South Carolina, high prevalence and abundance of the worm were found in spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura*), and highfin goby (*Gobionellus oceanicus*), and a high prevalence but lower abundance was found in mummichog (*Fundulus heteroclitus*). In Nova Scotia, 2 nematodes were found in a single specimen of tomcod (*Microgadus tomcod*). All of the infected species are associated with a benthic lifestyle, and some of them are known to move between estuaries along the coastline. Lower infection rates in Nova Scotia may be associated with lower water temperatures and/or higher salinity of the sampling site. Most of the L_3 were found encapsulated in mesenteric tissue around the intestine and stomach. No L_4 or pre-adult worms were found. Mean body length of the L_3 was smaller than L_3 stages found in American eels from Cape Breton. This suggests that development of *A. crassus* is arrested at the L_3 in the 5 fish species reported here, supporting their status as paratenic hosts.

The invasive swimbladder nematode, *Anguillicola crassus*, was first found and described in the Japanese eel (*Anguilla japonica*) in East Asia (Moravec and Taraschewski, 1988). The worm was first documented outside its native range in wild European eel *Anguilla anguilla* in Germany in 1982, and it has spread throughout Europe since then (Kennedy and Fitch, 1990; Moravec, 1992; Kangur et al., 2010). Copepods and ostracods act as intermediate hosts for the nematode larvae (De Charleroy et al., 1990; Moravec and Konecny, 1994). Given that the major food item is not copepods but fish for European eels larger than 50 cm (Tesch, 1977; De Nie, 1987), various fish species were assumed to act as paratenic hosts for *A. crassus* (De Charleroy et al., 1990; Moravec et al., 1993), which was verified when numerous freshwater and brackish forage fish species were found infected in Europe (Haenen and van Banning, 1990; Höglund and Thomas, 1992; Thomas and Ollevier, 1992; Székely, 1994). The ability of fish to act as paratenic hosts for *A. crassu*s was confirmed via experimental infection (De Charleroy et al., 1990; Moravec and Konecny, 1994; Székely, 1996) as well as the fact that eels could be infected by feeding on infected fish (Haenen and van Banning, 1991). The capacity to use paratenic hosts may in part account for the rapid spread of *A. crassus* in Europe (Székely et al., 2009).

This invasive parasite was first found in North America in 1995, occurring in captive eels from an aquaculture facility in southern Texas and a single wild-caught American eel (*Anguilla rostrata*) specimen from Winyah Bay, South Carolina (Fries et al., 1996). Thereafter, the nematode has been recorded in American eels from rivers along other parts of the eastern seaboard, including North Carolina in 1999 (Moser et al., 2001), Chesapeake Bay and the Hudson River watershed in 1997 (Barse and Secor, 1999), Massachusetts in 2003, and New Brunswick and Cape Breton, Nova Scotia, in 2007 (Aieta and Oliveira, 2009; Rockwell et al., 2009). Furthermore, prevalence was found to have increased in South Carolina over the past 15 years (Hein et al., 2014). These findings show that *A. crassus* has spread throughout much of eastern North America.

Forage fish may play an important role as paratenic hosts in the transmission of *A. crassus* to American eels as they do in European eels. However, paratenic hosts have never been found in North America to date. Therefore, forage fish from different areas along the eastern seaboard were examined to determine their potential role as paratenic hosts of *A. crassus* in North America. Sampling localities varied in salinity, as paratenic host have been reported both in fresh water (Haenen and van Banning, 1990; Thomas and Ollevier, 1992; Székely, 1994) and brackish water (Höglund and Thomas, 1992) in Europe.

MATERIALS AND METHODS

A total of 261 fish specimens belonging to 23 species, 18 families, and 12 orders, of a size suitable for eel prey (not exceeding 13 cm in standard body length) (Tesch, 1977; De Nie, 1987), were collected from 2 stretches of the Ashley River (mid-points of 32.948314°N, 80.167309°W and 32.893062°N, 80.117666°W) and 1 of the Cooper River (32.994336°N, 79.917509°W) in South Carolina and in the Mira River (46.047229°N, 60.019272°W) in Cape Breton, Nova Scotia, from August to December 2012 (Fig. 1). All areas were tidally influenced and were known for high prevalence and intensity of *A. crassus* in American eels (Rockwell et al., 2009; Denny et al., 2013; Hein et al., 2014). The more upstream part of the Ashley River (Ashley River A) covered a 2.7 km stretch and had salinities of 0.2–1.9 ppt when fish were collected, whereas the downstream part (Ashley River B) covered a 6.9 km stretch and had salinities of 0.1–0.7 ppt. Salinities in the 6.6 km stretch of Cooper River were 0.3–9.2 ppt during sample collection. South Carolina fish were captured along the riverbank

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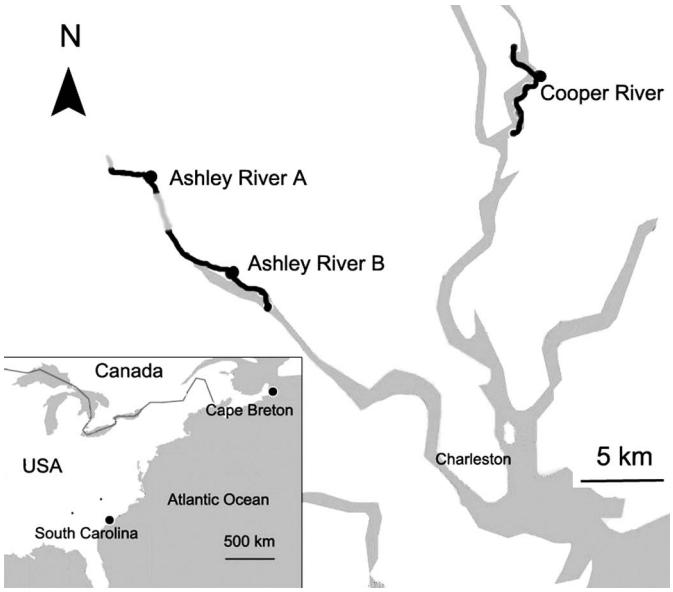

FIGURE 1. Three sampling localities (Ashley River A, Ashley River B, Cooper River) in South Carolina. Inset: Sampling location in South Carolina and Mira River, Cape Breton, Nova Scotia, Canada.

in depths ≤1.5 m during mid-ebb through early flood tidal stages using a Smith-Root electrofisher boat (Arnott et al., 2010). In the Mira River estuary, fish were caught using minnow traps or beach seines in salinities of 10–18 ppt. A sample of 15 yellow stage American eels was also collected from Mira River. All the fish were stored in a –80 C freezer for subsequent parasitological examination.

Each fish was thawed, weighed to the nearest 0.01 g, and standard body length measured to the nearest 1 ml. The swimbladder, intestine, and stomach were removed and placed in a Petri dish. Mesenteric tissues surrounding the intestine and stomach were separated using a hooked needle and examined for the presence of nematode larvae using a stereomicroscope. The swim bladder, intestine and stomach were opened and food contents in the latter 2 organs were discarded. The opened organs then were squashed between 2 glass plates and examined for the presence of larval nematodes using a stereomicroscope. Number and localization of larvae were recorded, and larvae were preserved in 5% formalin solution for morphological identification. For the American eels, only the swimbladder was removed for examination. It was screened for larval parasites, as above, after counting and removing any adult stages of the parasite from the swimbladder lumen.

Identification of the larval nematodes collected from forage fish and eels was based on the morphological descriptions of Moravec (2013). To compare developmental status of the larvae, body length and width of the worms were measured using a compound microscope fitted with a calibrated eyepiece graticule and compared statistically to the third-stage larvae (L_3) removed from the eels using a *t*-test.

Prevalence (the number of fish infected divided by the number of fish examined, expressed as a percentage) and mean abundance (the total number of *A. crassus* divided by the total number of fish examined) were calculated for each fish species at each sampling locality (Bush et al., 1997).

RESULTS

Among the 261 forage fish specimens that were examined, 35 individuals belonging to 5 species and 3 orders were found to be infected with L_3 of *A. crassus* (Table I). No L_4 or pre-adult *A. crassus* worms were found in any of the forage fish examined. In South Carolina, high prevalence and mean abundance of the nematode were found in spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura*), and highfin goby (*Gobionellus oceanicus*). All 4 specimens of mummichog (*Fundulus heteroclitus*) from South Carolina were also infected, but mean abundance was lower. In Cape Breton only 2 worms were found in a single specimen of the tomcod (*Microgadus tomcod*). In American eels from Cape Breton, L_3 occurred at 40% prevalence and 2.93 mean abundance, with those of L_4 and adults combined were 66.7% and 3.07.

Anguillicola crassus larvae collected from forage fish were morphologically similar to L_3 from American eels and fit the description from Moravec (2013). The nematode was identified as *A. crassus* by the typical V-shape sclerotized oral apparatus at the cephalic end and a conical tail with small cuticular spike at its tip (Fig. 2).

Most of the L_3 were found encapsulated in mesenteric tissue around the intestine and stomach, with a few worms also found in the intestinal wall (Fig. 3). In mummichog and eels, all the L_3 were found unencapsulated in the swimbladder wall.

The mean body length of L_3 from American eels was 877 μm (n = 18; range, 770–963). Mean body length of L_3 from the other 5 infected forage fish species was 830 μm (n = 55; range, 650–972), which was significantly different from those in eels ($P < 0.05$; Table II).

DISCUSSION

Although *A. crassus* is endemic to the Japanese eel in eastern Asia and has been reported from the European eel in Europe and the American eel in North America, fish paratenic hosts of the nematode have been identified thus far only in Europe (Haenen and van Banning, 1990; Höglund and Thomas, 1992; Thomas and Ollevier, 1992; Székely, 1994). In the present study, L_3 of *A. crassus* were found in 5 fish species, *L. xanthurus*, *B. chrysoura*, *G. oceanicus*, *F. heteroclitus,* and *M. tomcod*, suggesting that these fish act as paratenic hosts for *A. crassus* in North America.

Among the 23 fish species examined, only individuals of 5 species were found to be infected with the L_3 of *A. crassus*, with high prevalence and mean abundance in spot, silver perch, and highfin goby (Table I), which all belong to the perciformes. However, not all perciformes were infected, and infections were also found in a cyprinodont and a gadid (Table I). In Europe, larvae of *A. crassus* have previously been reported from 30 species of wild-caught fish belonging to 8 orders (Table III) (Haenen and van Banning, 1990; Höglund and Thomas, 1992; Thomas and Ollevier, 1992; Reimer et al., 1994; Székely, 1994). In addition, aquatic snails, amphibians, and larvae of aquatic insects were found to be suitable paratenic hosts for the L_3 in experimental infections (Moravec, 1996; Moravec and Škoríková, 1998). These findings suggest a low host specificity of *A. crassus* larvae and a lack of relationship with host phylogeny.

It has been suggested that the distribution of *A. crassus* is generally limited to fresh and brackish waters since the viability of free-living L_2 larvae is greatly diminished in marine conditions (De Charleroy et al., 1989; Moravec et al., 1993). In Europe, *A. crassus* larvae have been found in numerous freshwater fish species (Haenen and van Banning, 1990; Thomas and Ollevier, 1992; Székely, 1994) as well as 2 brackish species, the deep-snouted pipefish (*Syngnathus typhle*) and black goby (*Gobius niger*) (Höglund and Thomas, 1992; Reimer et al., 1994). The 5 infected fish we identified all inhabit a wide range of salinities, demonstrating that forage fishes in brackish waters of North

TABLE I. Prevalence (P, %) and mean abundance (M, ±SD) of L_3 larvae of *Anguillicola crassus* in fish from Cooper River, Ashley River A, Ashley River B in South Carolina, and Mira River in Cape Breton, Canada. N, number of fish examined; L, mean standard length and standard deviation (cm) of fish.

	Cooper River				Ashley River A				Ashley River B				Mira River			
Order and species (common name)	N	L	P	M	N	L	P	M	N	L	P	M	N	L	P	M
Atheriniformes																
Menidia menidia (Atlantic silverside)	5	4.5 ± 1.0	0	0	2	5.2	0	0	2	4.0	0	0	8	7.1 ± 1.2	0	0
Cypriniformes																
Notemigonus crysoleucas (Golden shiner)	—				—				1	7.2	0	0	—			
Cyprinodontiformes																
Fundulus heteroclitus (Mummichog)	—				2	6.1	100	1.0	2	6.5	100	4.0	13	6.4 ± 1.0	0	0
Clupeiformes																
Anchoa mitchilli (Bay anchovy)	30	4.1 ± 0.5	0	0	—				6	4.1 ± 0.6	0	0	—			
Brevoortia tyrannus (Atlantic menhaden)	1	5.1	0	0	—				—				—			
Dorosoma petenense (Threadfin shad)	—				—				1	5.5	0	0	—			
Gadiformes																
Microgadus tomcod (Atlantic tomcod)	—				—				—				9	9.9 ± 0.7	11	0.2 ± 0.6
Gasterosteiformes																
Apeltes quadracus (4-spine stickleback)	—				—				—				28	3.3 ± 0.6	0	0
Gasterosteus aculeatus (3-spine stickleback)	—				—				—				6	3.2 ± 0.3	0	0
Mugiliformes																
Mugil cephalus (Striped mullet)	—				—				6	9.8 ± 1.6	0	0	—			
Perciformes																
Bairdiella chrysoura (Silver perch)	5	8.4 ± 0.9	80	24.2 ± 28	—				7	8.4 ± 1.7	85.7	13.4 ± 14	—			
Eucinostomus gula (Jenny morjarra)	3	6.2 ± 1.2	0	0	—				14	4.9 ± 0.7	0	0	—			
Gobionellus oceanicus (Highfin goby)	13	8.8 ± 0.5	38.5	35.9 ± 60					—				—			
Lagodon rhomboids (Pinfish)	25	8.4 ± 1.4	0	0	—				6	8.1 ± 0.9	0	0	—			
Leiostomus xanthurus (Spot)	—				8	8.5 ± 0.3	100	78.1 ± 30	8	7.7 ± 2.6	87.5	85.5 ± 54	—			
Lepomis auritus (Redbreast sunfish)	—				6	10.7 ± 1.3	0	0	—				—			
Lepomis macrochirus (Bluegill)	—				16	8.5 ± 2.5	0	0	1	9.2	0	0	—			
Lepomis microlophus (Redear sunfish)	—				5	6.8 ± 1.2	0	0	—				—			
Pleuronectiformes																
Citharichthys spilopterus (Bay whiff)	—				—				4	8.4 ± 0.1	0	0	—			
Trinectes maculatus (Hogchoker)	—				—				1	6.2	0	0	—			
Scorpaeniformes																
Myoxocephalus aenaeus (Grubby)	—				—				—				9	8.7 ± 1.0	0	0
Siluriformes																
Ictalurus furcatus (Blue catfish)	—				—				1	10.2	0	0	—			
Syngnathiformes																
Syngnathus fuscus (Northern pipefish)	—				—				—				7	13.0 ± 2	0	0

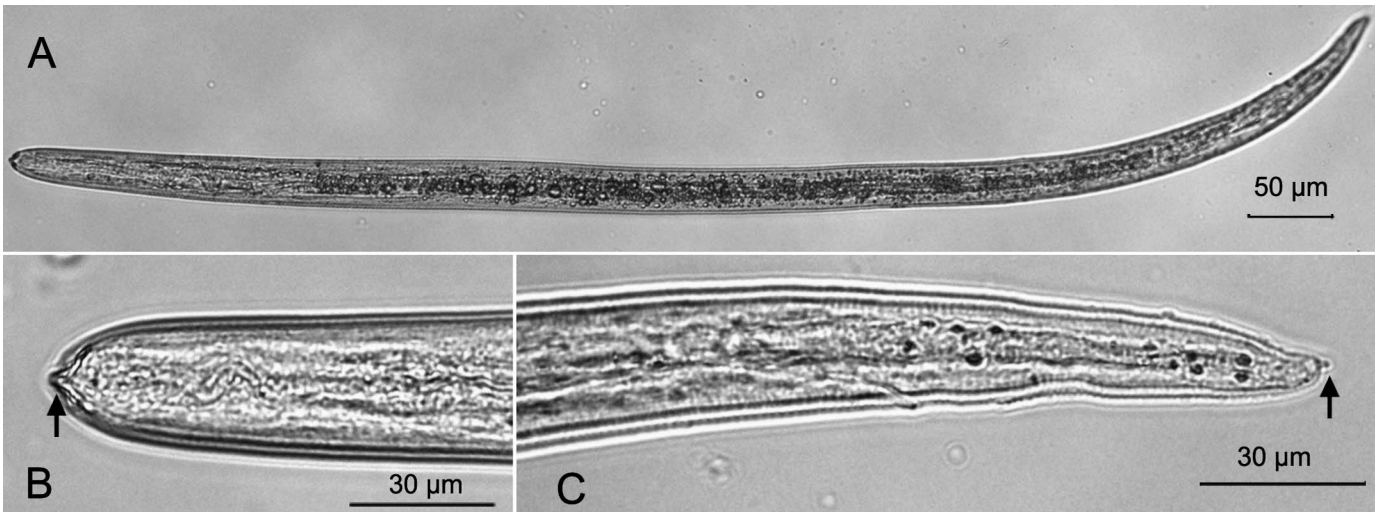

FIGURE 2. Third-stage larvae of *Anguillicola crassus*. **(A)** whole worm; **(B)** cephalic end with v-shape sclerotized oral apparatus (arrow); **(C)** conical tail with small spike at its tip (arrow).

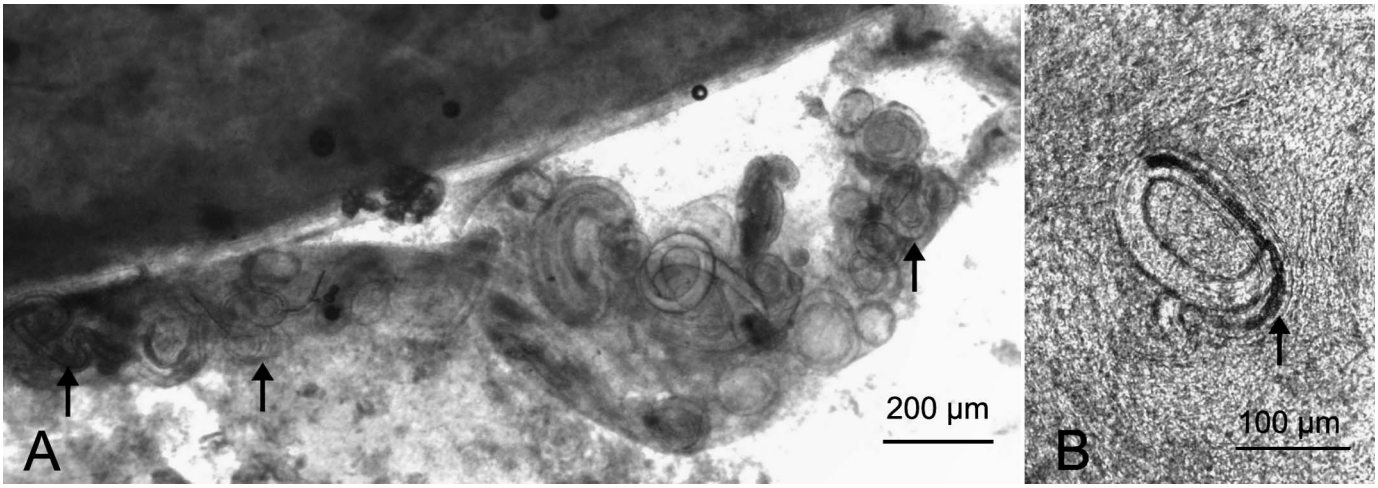

FIGURE 3. In situ third-stage larvae of *Anguillicola crassus* in paratenic fish hosts. **(A)** encapsulated larvae (arrows) in mesenteric tissue surrounding the intestine of an individual of *Gobionellus oceanicus*; **(B)** encapsulated larva (arrow) in the intestinal wall of an individual of *Bairdiella chrysoura*.

America can serve as paratenic hosts, as do their counterparts in Europe. Some of the infected species in our study are capable of moving long distances, both within and between estuaries. For example, spot use upper estuarine habitats as nursery areas, but as they grow they move downstream toward higher salinity areas, and they have seasonal migrations along the coastline (Pacheco, 1962). Conversely, mummichog typically move very short distances (Abraham, 1985), so the infected specimens likely acquired *A. crassus* near their sites of collection. Since some of the fish species show extensive movement patterns, they may serve as

TABLE II. Mean measurements (±SD; in µm) and range of L_3 larvae of *Anguillicola crassus* in American eel (*Anguilla rostrata*) and 5 species of paratenic hosts.

Host	Species	n	Body length ± SD	Range	Body width ± SD	Range
Definitive	*Anguilla rostrata*	18	877 ± 59	770–963	34 ± 5	26–44
Paratenic	*Microgadus tomcod*	1	846	—	33	—
	Gobionellus oceanicus	21	824 ± 54	705–919	30 ± 2	27–33
	Fundulus heteroclitus	6	809 ± 128	650–950	32 ± 1	31–34
	Bairdiella chrysoura	12	823 ± 76	698–904	31 ± 3	26–36
	Leiostomus xanthurus	15	852 ± 75	727–972	30 ± 2	27–34
Total paratenic		55	830 ± 70	650–972	30 ± 1	26–36

TABLE III. Mean abundance of L_3 larvae of *Anguillicola crassus* in fish paratenic hosts reported in fresh waters (FW) and brackish waters (BW) in Europe. For Höglund and Thomas (1992), mean abundance based on the reported mean intensity, infected and total fish number.

	Mean abundance				
Order and species (common name)	Haenen and Banning, 1990 (FW)	Thomas and Ollevier, 1992 (FW)	Székely, 1994 (FW)	Höglund and Thomas, 1992 (BW)	Reimer et al., 1994 (BW)
Cypriniformes					
Abramis brama (Bream)			1.2		
Alburnus alburnus (Bleak)		0.2	9.4	<1	
Aspius aspius (Asp)			12.3		
Blicca bjoerkna (White bream)			6.9		
Carassius auratus gibelio (Gibel carp)			2.1		
Chondrostoma nasus (Common nase)		1.7			
Cyprinus carpio (Common carp)			18.3		
Gobio gobio (Gudgeon)		11	1.0		
Leuciscus idus (Ide)		0.07			
Leuciscus leuciscus (Dace)		2			
Pseudorasbora parva (Chinese rasbora)			3.1		
Rhodeus amarus (Bitterling)			2.9		
Rutilus rutilus (Roach)		0.01	11.2		
Scardinius erythrophthalmus (Rudd)		0.06	9.8		
Squalius cephalus (Chub)		3			
Tinca tinca (Tench)		0.02	3.8		
Cyprinodontiformes					
Lebistes reticulatus (Guppy)*					?
Esociformes					
Esox Lucius (Pike)			0.1		
Gasterosteiformes					
Ameiurus nebulosus (Brown bullhead)		9.2			
Gasterosteus aculeatus (3-spined stickleback)	1	1.4			
Osmeriformes					
Osmerus eperlanus (Smelt)	3.4				
Perciformes					
Gobius niger (Black goby)				13	<1
Gymnocephalus cernuus (Ruffe)	2.5	19.7	62.8	11	
Lepomis gibbosus (Pumpkinseed)		13.4	2.0		
Neogobius fluviatilis (River goby)			7.9		
Oreochromis niloticus (Tilapia)		0.5			
Perca fluviatilis (Perch)	1.2	0.8	2.0	<1	
Sander lucioperca (Pike perch)	0.4	1.9	0.2		
Siluriformes					
Silurus glanis (Europe catfish)			214.1		
Syngnathiformes					
Syngnathus typhle (Pipefish)					?

* Cited in Reimer et al. (1994).

important vectors between eel habitats (Höglund and Thomas, 1992) and may contribute significantly to the dispersal of *A. crassus* along the eastern seaboard of North America, in addition to any dispersal associated with natural movement of eels (Kirk et al., 2000).

Feeding ecology likely plays an important role in determining whether fish are exposed to *A. crassus*. Free-living L_2 larvae of *A. crassus* sink to the bottom, where they may infect potential fish prey such as small crustaceans. Infection levels in fish are reported to be highest near the bottom (Thomas and Ollevier, 1992), and some of the fish species previously found to be most heavily infected by *A. crassus*, such as black goby, ruffe, gudgeon, and brown bullhead (Table III), are benthic feeders (Höglund and Thomas, 1992; Thomas and Ollevier, 1992). In our study all 5 of the infected fish species are associated with benthic habitats, and they have diets that typically comprise small crustaceans and other benthic-associated organisms (Stickney et al., 1975; Stewart and Auster, 1987). Given that the first intermediate hosts of *A. crassus* are small crustaceans (i.e., copepods and ostracods) (De Charleroy et al., 1990; Moravec and Konecny, 1994), the feeding characteristics of these fishes most likely contributed to their exposure to L_3 of *A. crassus* borne by these crustaceans.

Among the 4 sampling localities, the heavily infected fish species were found in South Carolina, whereas only 1 individual was found to be lightly infected in Cape Breton. Although Aieta and Oliveira (2009), Rockwell et al. (2009), and Denny et al. (2013) all found a high prevalence of adult *A. crassus* in American eels from northern Nova Scotia and New Brunswick, the development and viability of egg, larval and adult stages of *A. crassus* are temperature-dependent and inhibited at low temperatures (Thomas and Ollevier, 1993; Knopf et al., 1998). Mean water temperatures are much lower at Cape Breton than South Carolina due to their latitudinal separation (~46°N and ~33°N, respectively), so the lower infection levels in Cape Breton may have been due to lower water temperatures inhibiting larval infectivity or survival of intermediate hosts. In addition, the higher salinity of the Cape Breton locality (10–18 ppt) may also have contributed to the lower infection levels of the worm found there compared with South Carolina (≤9 ppt), since transmission of the parasite declines with increasing salinity (Kirk et al., 2000).

Body length of L_3 varied greatly in fishes from different studies. In experimental infections of 4 fish species, body length of L_3 ranged from 0.98 to 1.02 mm (Moravec and Konecny, 1994). In field investigations, mean body length of L_3 was less than 0.7 mm in 4 freshwater fish species in the Netherlands (Haenen and Banning, 1990), but more than 0.87 mm in 7 freshwater fish species in Belgium (Thomas and Ollevier, 1992). In the present study, although body length of the L_3 found in forage fish was smaller than those found in American eels from Cape Breton, but it also varied from 650 to 972 μm.

In conclusion, our study is the first to identify paratenic hosts of *A. crassus* in North America. Of the 23 forage fish species belonging to 12 orders that we examined, individuals of 5 species belonging to 3 orders were found to be infected by L_3 of the parasite. Infection occurred in fish with benthic lifestyles, and the parasite was more prevalent and abundant in South Carolina compared to Novia Scotia, possibly due to differences in water temperature regimes and/or the salinity of the collection localities. The paratenic host species may act as vectors that contribute towards the dispersal of *A. crassus* along the eastern seaboard of North America.

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