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Distribution, prevalence, and intensity of the swim bladder parasite *Anguillicola crassus* in New England and eastern Canada

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ABSTRACT: In the summer of 2005, yellow phase American eels *Anguilla rostrata* were examined for the swim bladder parasite *Anguillicola crassus* from 26 locations in New England, USA, ranging from the Pawcatuck River, Rhode Island, to the East Machias River, Maine. An additional 12 sites were sampled within Canada during the summers of 2006 and 2007: 7 sites in southern Nova Scotia and 5 sites within the St. Lawrence River system. In 2007, eels were also obtained from New Brunswick, northern Nova Scotia, Prince Edward Island, and Newfoundland through the commercial eel fishery. All locations in Rhode Island (n = 3) and Massachusetts (n = 10) and 7 in Maine (n = 13) had infected eels, with parasite prevalence ranging from 7 to 76%. No eels sampled from southern Nova Scotia or the St. Lawrence River system were infected with the parasite. New Brunswick and northern Nova Scotia had infected eels ranging from 3 to 30% parasite prevalence, with Cape Breton, Nova Scotia, being the furthest north the parasite has been reported in American eels. There was no significant relationship between parasite prevalence and latitude. The present study supports the hypothesis that the parasite is capable of expanding its range further into the Maritimes and could potentially reach the St. Lawrence River system.

KEY WORDS: *Anguilla rostrata* · *Anguillicola crassus* · Parasite · Swimbladder · Range · New England · Canada

INTRODUCTION

The American eel *Anguilla rostrata* is the only species of *Anguilla* that lives in North America, occupying freshwater, estuarine, and marine habitats (Tesch 2003). Historically, it has been an extremely successful species, in part, because of its large native range, great diversity of habitats, and dietary generalist behavior (Helfman et al. 1987). Recent evidence suggests that the *A. rostrata* population is declining at the northern extent of its range, particularly in the Lake Ontario–St. Lawrence River area (Castonguay et al. 1994) and in the USA (Richkus & Whalen 1999). Several factors have been suggested as contributing to eel decline: chemical contamination, habitat modifications, commercial fishing, and oceanic changes (Castonguay et al. 1994, Haro et al. 2000, Friedland et al. 2007). The recent introduction of the swim bladder parasite *Anguillicola crassus* into North America is another factor that must now be considered (Haro et al. 2000).

Anguillicola crassus is a nematode that establishes itself in the swim bladder of an anguillid eel via ingestion of an infected intermediate freshwater ostracod (Pietrock & Meinelt 2002, Moravec 2004), calanoid (Pietrock & Meinelt 2002), cyclopoid copepod (De Charleroy et al. 1990), or one of many paratenic fish species (Johnson et al. 1995). In the European eel *Anguilla anguilla*, the parasite has been shown to cause an array of serious problems that include internal bleeding (Mellergaard & Dalsgaard 1989), inflammatory reactions (Molnár 1994) and dilation of blood vessels, formation of granuloma, and thickening of the entire swim bladder wall (Würtz & Taraschewski 2000). Swim bladders have often been found to be irreversibly damaged due to the lumen becoming filled with dead *A. crassus*, digested blood, and debris, as

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well as the swim bladder wall becoming full of encapsulated adults and juveniles (Kirk 2003). Studies examining the effects of the parasite on American eels are limited. Ooi et al. (1996) found infected American eels raised in a Taiwanese fish farm had hemorrhaged and ruptured swim bladders, anemia, and peritonitis due to internal parasite migration. Similarly, Sokolowski & Dove (2006) found pathological conditions in infected eels to include blood-filled swim bladders and deleterious alterations of the submucosa, mucularis, serosa, and lamina propria of the swim bladder wall.

When Japanese eels were imported from Asia to Europe for evaluation in aquaculture in the 1980s (Johnson et al. 1995), the imported eels led to the establishment of *Anguillicola crassus* in the European eel (Gollock et al. 2004). More recently, the parasite has been identified in the American eel. Although the first reports were from a Texas aquaculture facility in 1994 (Johnson et al. 1995), subsequent investigation showed the source of these eels to be elvers transferred from South Carolina (Fries et al. 1996), indicating an east coast origin for the parasite. In 1997, fishers found *A. crassus* in American eels in a tributary in the mid-Chesapeake Bay and, subsequently, in tributaries of the Chesapeake Bay and Hudson River (Barse & Secor 1999), as well as within the Hudson River estuary (Morrison & Secor 2003).

During the summer of 2003, *Anguillicola crassus* was discovered in yellow eels from the Paskamansett River, Dartmouth, Massachussetts (K. Oliveira unpubl. data). The parasite had never been recorded this far north in the American eel range. Considering the potential effects of this introduction on American eels and the parasite's history of rapid range expansion, the present study was conducted to explore the current distribution of the parasite in New England, the Maritime Provinces, and the St. Lawrence River.

MATERIALS AND METHODS

During the summer of 2005, yellow eels *Anguilla rostrata* were collected from 26 sites within New England, 3 of the sites were in Rhode Island, 10 in Massachusetts, and 13 in Maine (Fig. 1, see Table 1). Sampling further south was not deemed necessary as it had been determined that the parasite was already established within the Connecticut River (S. Gephard, CT Department of Environmental Protection, pers. comm.). During the summer of 2006, yellow eels were collected from 5 rivers in Nova Scotia and 5 locations within the St. Lawrence River system, 3 being tributaries and 2 being dams in the main stem of the river (Fig. 1, see Table 1). Eels were collected from all riverine sites by electrofishing from June to September. Sites were similar in general characteristics; all were coastal and above the head of tide (freshwater), depth <50 cm, low to moderate flow, but varied between predominantly sandy to predominantly rocky substrate. Due to difficulty accessing freshwater areas within the Kennebec River, Maine, 25 estuarine yellow phase eels were obtained from eel pots set in the estuary. Eels collected from the Beauharnois Dam in Quebec and the Moses-Saunders Dam in Ontario were captured while ascending the eel ladders at those facilities. Latitude and longitude were recorded at each site using a handheld GPS unit. Only yellow phase eels, the primary feeding stage, were collected during electrofishing and dam collections.

In the summer of 2007, 4 rivers in Nova Scotia were resampled (Beaver, Salmon, Metaghan, and Coques) and 2 additional rivers (Sissiboo and West) were considered to expand the sampling range (Fig. 1, see Table 1). In addition, commercially collected eels from the Maritime Provinces of New Brunswick, northern Nova Scotia, Prince Edward Island (PEI), and Newfoundland were also sampled at the South Shore Trading processing plant (Port Elgin, New Brunswick) (Fig. 1, see Table 2). Whole eels from PEI and Newfoundland were not available, so our examination of these locations was limited to whole freshly removed swim bladders.

After collection, eels were killed by immersion in clove oil (Eugenol). Eel weight (g) and total length (mm) were recorded. The swim bladder was dissected 0 to 6 d after collection and opened for analysis of infection. Eels not dissected within 24 h of collection were slit from anus to head and placed in 70 to 80% isopropyl alcohol for temporary preservation until examination. The swim bladders from PEI and Newfoundland eels were preserved in 70% isopropyl and then examined using the same procedures as swim bladders from whole eels. Eels were assessed for prevalence, i.e. the numbers of infected eels divided by the total number of eels examined, and mean intensity, i.e. the average number of nematodes found among the infected eels (Bush et al. 1997). Only nematodes found in the lumen were examined in the present study. These intact and partial lumen nematodes were counted and placed in vials containing 70 to 85% ethanol. Parasite identifications were made using a dissecting microscope and the descriptions of Kuwahara et al. (1974), Moravec & Taraschewski (1988), and Moravec (2004). Voucher specimens were deposited at the US National Parasite Collection (USNPC No. 101411.00).

Data from the eels from the fishery samples were known to have several limitations: (1) the location of capture was limited to the river or general region and no GPS data were available, (2) the eels were all of commercial size (>300 mm) and not representative of

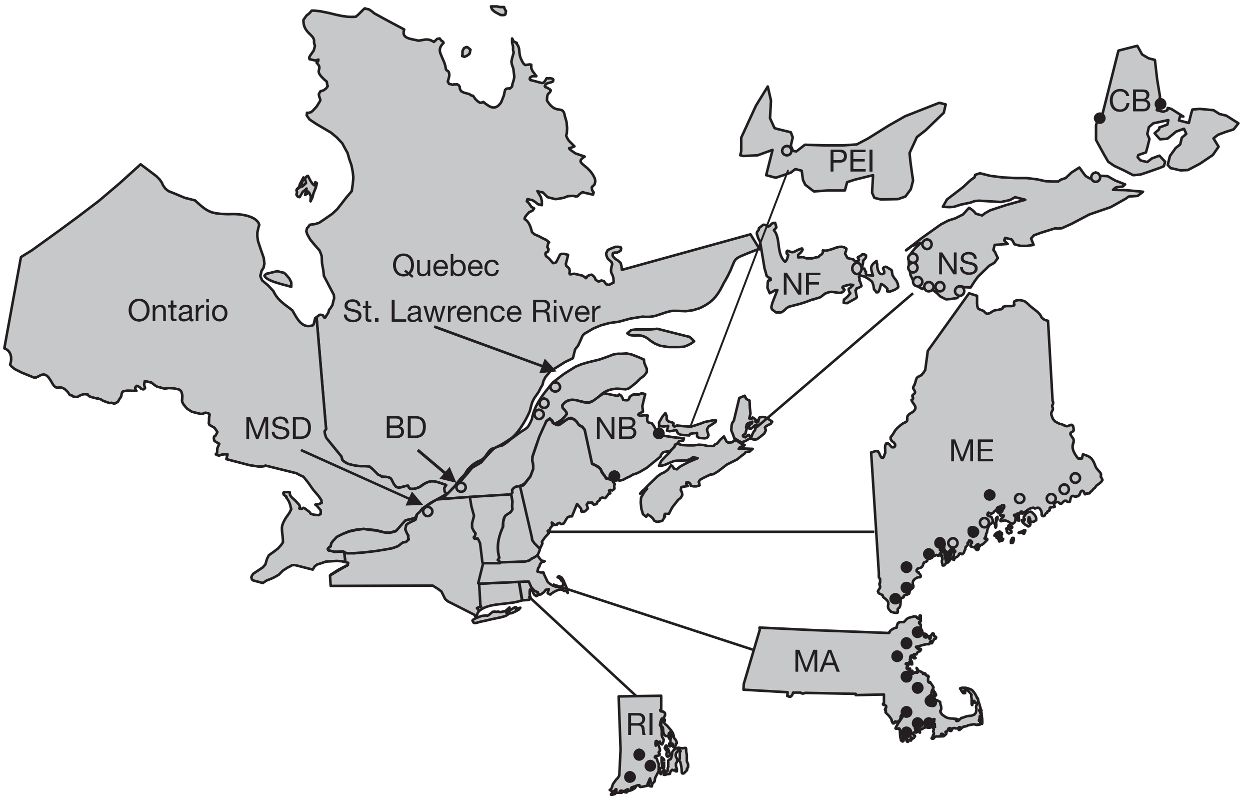

Fig. 1. Collection locations of American eels *Anguilla rostrata* in the United States and Canada. BD: Beauharnois Dam in Quebec; CB: Cape Breton Island; MA: Massachusetts; ME: Maine; MSD: Moses Saunders Dam in Ontario; NB: New Brunswick; NF: Newfoundland; NS: Nova Scotia; PEI: Prince Edward Island; RI: Rhode Island; ○: sites without the parasite *Anguillicola crassus*; ●: sites with the parasite

the overall size distribution of the sampling location, and (3) only swim bladders were available for eels from PEI and Newfoundland.

Data were analyzed with SPSS 13.0 for Windows. The Pearson correlation model was used to examine the relationship between latitude and prevalence and to explore relationships between prevalence and intensity. Significance was accepted for all tests at the $p \leq 0.05$ level.

RESULTS

The parasite *Anguillicola crassus* had a consistent distribution throughout most of the New England sampling locations; it was found at all 3 sites in Rhode Island and at all 10 sites in Massachusetts, with the maximum prevalence being 76% in the Neponset River, Massachussetts. The prevalence of infection in Maine ranged from 0% to a high of 65% in eels *Anguilla rostrata* collected from the Kennebunk River (Table 1). The northernmost site in the USA with infected eels was the Sedgeunkedunk Stream, a tributary of the Penobscot River, Maine. The parasite exhibited a more disjunctive distribution in Canadian locations, with no parasites being found at locations within the St. Lawrence River or in southern Nova Scotia. A single parasite was found within an eel from the St. Johns River and Silver Lake, New Brunswick, but several parasitized eels were present in northern Nova Scotia (Table 2).

Due to data limitations, the distribution analysis was limited to the New England sites. Correlation analysis of the relationship between latitude and the prevalence of infection was limited to the range of the parasite (Pawcatuck River, Rhode Island, to Penobscot River, Maine), with the Penobscot latitude adjusted to the mouth of the river (44° 22.150′ N). The Nova Scotia locations were also omitted to remove any complicating longitudinal component from the analysis. This analysis revealed no significant correlation between latitude and the prevalence of infection (Pearson correlation = −0.32, 2-tailed significance $p = 0.147$). There was a strong positive correlation between the prevalence of infection and mean intensity (Pearson correlation = 0.81, 2-tailed significance $p < 0.001$), confirming that sites of higher prevalence had higher mean parasite intensity.

Yellow eels, collected from all locations, ranged in length from 56 to 699 mm (n = 1324 eels; mean ± SD = 248.8 ± 101.4 mm). Infected eels ranged in length from 70 to 594 mm (n = 315 eels; mean ± SD = 242.9 ± 88.5 mm), with parasite intensity ranging from 1 to 18 parasites eel^{-1} (mean ± SD = 3.2 ± 2.8). Non-parasitized eels from locations that had parasitized eels ranged in size from 56 to 699 mm (n = 403 eels; mean ± SD = 203.9 ± 93.8 mm). The significant difference in mean eel size among rivers prevented comparisons of prevalence and intensity from being made among locations.

DISCUSSION

Data from all collections indicate that the parasite *Anguillicola crassus* has at least spread to Cape Breton Island, Nova Scotia, on the east coast of North America.

Table 1. *Anguillicola crassus*, *Anguilla rostrata.* Summary of the prevalence and mean intensity of *A. crassus* in eels *A. rostrata* for all locations sampled in the USA and Canada. Values for intensity, length and weight are mean ± SD and range (in parentheses)

Location	Lat., Long.	No. of eels (n)		Prevalence (%)	Intensity	Eel length (mm)		Eel weight (g)	
		Collected	Infected			Non-infected	Infected	Non-infected	Infected
Rhode Island									
Pawcatuck River	41° 26.27′ N, 71° 43.32′ W	29	20	69	2.6 ± 2.4 (1–11)	125.3 ± 8.3 (112–137)	183.1 ± 111.5 (102–530)	2.6 ± 0.8 (1–4)	27.7 ± 73.6 (2–324)
Gilbert Stuart Brook	41° 31.18′ N, 71° 26.67′ W	71	25	35	2.2 ± 1.6 (1–7)	202.5 ± 73.0 (56–375)	245.8 ± 59.1 (125–327)	8.0 ± 19.1 (1–90)	26.8 ± 17.2 (2–60)
Annaquatucket River	41° 33.03′ N, 71° 26.45′ W	29	8	28	3.5 ± 1.9 (1–6)	232.9 ± 79.9 (77–322)	232.8 ± 84.5 (142–376)	29.5 ± 22.4 (1–75)	28.3 ± 26.5 (3–75)
Massachusetts									
Slocums River	41° 34.29′ N, 71° 00.27′ W	69	44	64	2.9 ± 1.7 (1–8)	244.7 ± 59.6 (138–335)	234.2 ± 45.5 (160–310)	17.2 ± 22.9 (4–74)	13.3 ± 21.3 (5–64)
Westport River	41° 38.03′ N, 71° 03.82′ W	33	11	33	2.8 ± 1.6 (1–5)	185.8 ± 40.6 (114–250)	177.1 ± 52.5 (70–252)	9.8 ± 6.5 (2–23)	9.8 ± 8.4 (1–29)
Acushnet River	41° 41.01′ N, 70° 55.17′ W	45	26	58	3.6 ± 3.9 (1–18)	276.1 ± 125.5 (92–699)	276.2 ± 57.1 (140–362)	61.2 ± 127.6 (1–580)	41.9 ± 21.6 (4–79)
Weweantic River	41° 46.79′ N, 70° 45.79′ W	19	4	21	3.3 ± 2.6 (1–7)	235.3 ± 55.8 (155–322)	288.0 ± 64.5 (156–299)	21.6 ± 17.3 (4–57)	21.1 ± 19.3 (5–45)
Eel River	41° 55.06′ N, 70° 37.58′ W	43	23	53	3.1 ± 2.0 (1–7)	276.6 ± 83.3 (127–492)	295.0 ± 131.6 (126–594)	48.0 ± 48.1 (2–206)	76.6 ± 98.1 (3–345)
South River	42° 05.86′ N, 70° 43.07′ W	44	7	16	3.0 ± 1.2 (2–5)	193.2 ± 77.9 (66–343)	253.3 ± 63.9 (116–320)	8.4 ± 20.2 (1–85)	31.1 ± 18.5 (2–65)
Neponset River	42° 15.73′ N, 71° 02.83′ W	37	28	76	5.3 ± 4.2 (1–14)	223.0 ± 66.0 (116–297)	108.1 ± 57.1 (113–329)	27.1 ± 20.4 (2–59)	21.1 ± 18.7 (2–78)
Danvers River	42° 34.20′ N, 70° 55.68′ W	21	13	62	3.5 ± 2.7 (1–9)	183.5 ± 58.1 (112–282)	235.4 ± 101.7 (85–392)	11.6 ± 12.5 (1–37)	33.7 ± 40.0 (1–118)
Annisquam River	42° 36.59′ N, 70° 42.54′ W	27	9	33	2.0 ± 1.3 (1–5)	108.7 ± 72.4 (61–389)	198.6 ± 102.7 (101–381)	6.3 ± 24.1 (1–103)	24.0 ± 37.1 (1–99)
Parker River	42° 44.97′ N, 70° 55.71′ W	56	4	7	1.8 ± 1.5 (1–4)	133.8 ± 89.6 (71–376)	134.0 ± 100.3 (77–284)	9.4 ± 18.7 (1–87)	8.6 ± 16.3 (1–33)
Maine									
York River	43° 10.39′ N, 70° 46.28′ W	30	16	53	3.4 ± 2.6 (1–10)	210.1 ± 53.7 (100–296)	226.8 ± 59.0 (76–311)	17.9 ± 16.3 (1–58)	22.9 ± 16.1 (1–63)
Kennebunk River	43° 25.50′ N, 70° 33.83′ W	37	24	65	4.5 ± 3.1 (1–10)	219.9 ± 56.9 (137–307)	263.8 ± 72.6 (140–430)	19.6 ± 15.9 (3–49)	40.0 ± 33.5 (3–156)
Nonesuch River	43° 35.15′ N, 70° 27.89′ W	19	11	58	1.4 ± 0.7 (1–3)	206.4 ± 45.9 (161–285)	233.5 ± 62.5 (125–311)	13.8 ± 11.5 (6–39)	26.0 ± 19.0 (2–59)
Kennebec River	43° 54.82′ N, 69° 48.26′ W	25	15	60	3.7 ± 3.2 (1–11)	291.4 ± 44.7 (242–364)	304.6 ± 59.7 (246–445)	40.3 ± 16.2 (22–72)	51.7 ± 32.2 (25–136)
St. George River	44° 07.41′ N, 69° 14.80′ W	49	17	35	1.9 ± 1.1 (1–4)	180.9 ± 76.3 (67–343)	231.2 ± 88.7 (71–361)	15.1 ± 17.2 (1–69)	30.9 ± 25.4 (1–76)
Medomak River	44° 08.70′ N, 69° 24.95′ W	33	0	0	0	317.5 ± 106.8 (126–531)	– –	71.4 ± 66.5 (3–246)	– –
Ducktrap River	44° 19.76′ N, 69° 03.65′ W	14	0	0	0	303.2 ± 124.3 (101–510)	– –	67.8 ± 77.2 (1–254)	– –
Sheepscot River	44° 21.52′ N, 69° 32.71′ W	16	5	31	1.6 ± 0.9 (1–3)	321.9 ± 99.5 (176–500)	355 ± 144.3 (150–507)	65.5 ± 61.5 (6–221)	105.3 ± 99.7 (5–228)
Union River	44° 32.00′ N, 68° 24.60′ W	19	0	0	0	289.2 ± 102.4 (97–445)	– –	56.2 ± 48.5 (2–175)	– –

Table 1. (continued)

Location	Lat., Long.	No. of eels (n) Collected	Infected	Prevalence (%)	Intensity	Eel length (mm) Non-infected	Infected	Eel weight (g) Non-infected	Infected
Tunk Stream	44° 36.49′ N, 67° 59.75′ W	10	0	0	0	303.5 ± 130.8 (111–595)	– –	84.1 ± 124.8 (2–427)	– –
Pleasant River	44° 41.73′ N, 67° 44.52′ W	27	0	0	0	229 ± 78.5 (95–345)	– –	26.7 ± 24.2 (1–82)	– –
Penobscot River	44° 45.31′ N, 68° 46.17′ W	19	5	26	1.4 ± 0.9 (1–3)	219.1 ± 167.5 (86–545)	386.2 ± 173.2 (102–561)	48.2 ± 77.7 (1–255)	142.2 ± 124.7 (1–335)
East Machias River	45° 00.05′ N, 67° 37.09′ W	15	0	0	0	364.2 ± 74.6 (247–551)	– –	95.8 ± 74.5 (25–320)	– –
Nova Scotia									
West River	43° 44.71′ N, 65° 09.40′ W	24	0	0	0	261.7 ± 32.2 (175–307)	– –	30.4 ± 10.9 (10–45)	– –
Chebogue River	43° 50.48′ N, 66° 03.49′ W	19	0	0	0	251.0 ± 73.8 (110–335)	– –	36.6 ± 24.80 (5–80)	– –
Beaver River[a]	43° 59.89′ N, 66° 08.73′ W	78	0	0	0	273.1 ± 56.3 (160–480)	– –	39.5 ± 29.9 (5–215)	– –
Salmon River[a]	44° 03.29′ N, 66° 09.17′ W	81	0	0	0	284.0 ± 69.0 (110–465)	– –	45.3 ± 30.4 (5–140)	– –
Metaghan River[a]	44° 12.71′ N, 66° 07.88′ W	77	0	0	0	261.2 ± 39.9 (110–327)	– –	33.2 ± 14.5 (5–70)	– –
Grosses Coques River[a]	44° 22.47′ N, 66° 04.47′ W	47	0	0	0	247.1 ± 72.7 (80–360)	– –	31.6 ± 24.3 (5–105)	– –
Sissiboo River	44° 24.56′ N, 65° 59.76′ W	33	0	0	0	223.9 ± 54.9 (137–347)		24.6 ± 22.3 (5–100)	
Ontario									
Moses-Saunders Dam[b]	45° 00.35′ N, 74° 47.78′ W	60	0	0	0	367.8 ± 70.6 (250–610)	– –	66.9.8 ± 53.5 (10–315)	– –
Quebec									
Beauharnois Dam[b]	45° 18.89′ N, 73° 54.82′ W	25	0	0	0	336.2 ± 66.4 (245–450)	– –	55.4.0 ± 33.0 (20–120)	– –
Verte River[b]	48° 00.44′ N, 69° 20.75′ W	9	0	0	0	218.3 ± 131.9 (75–405)	– –	38.2 ± 45.0 (4–110)	– –
Trois Pistoles[b]	48° 05.73′ N, 69° 12.79′ W	13	0	0	0	367.7 ± 163.5 (110–675)	– –	155.4 ± 201.4 (5–695)	– –
Riviere Sud-Ouest[b]	48° 21.12′ N, 68° 45.68′ W	22	0	0	0	311.4 ± 92.4 (185–650)	– –	68.2 ± 104.9 (10–525)	– –

[a]Locations that were sampled in both 2006 and 2007. [b]Locations within the St. Lawrence River

Although the survey of the St. Lawrence River system was not exhaustive, it was comprehensive in its coverage and should have detected the parasite if present. The 3 tributaries within Quebec are representative of the lower St. Lawrence region, while the other 2 sites (Beauharnois and Moses-Saunders eel ladders) consisted of samples of upstream migrating eels *Anguilla rostrata* that were at least 6 yr old (K. Oliveira unpubl. data on age). The absence of the parasite in some sampled locations is probably not due to differences in eel size distribution. All eel collections in the present study included eels of multiple size classes, which should have allowed the detection of the parasite, if it had been present at each site.

All of the sites in the present study were sampled in the summer months, and Maine, in particular, was sampled within a 2 wk period. During this time the parasite is presumably most active and infective. A study of infection in the Elbe River in Germany did not depict any clear seasonal fluctuations in the parasite prevalence (Möller et al. 1991). Although parasite seasonality does not appear to have masked the presence of adult nematodes at the northernmost sites, it cannot be ruled out. Further study using a temporally staggered sampling design would be required to determine whether parasite prevalence varies seasonally.

The distribution of *Anguillicola crassus* in yellow eels collected from sites throughout New England depicted no significant correlation between latitude and the prevalence of infection, as has been noted in a previous study of American eels in North Carolina (Moser et al. 2001). The distribution and range may be the result of the parasite having >1 transport mechanism. The current range of *A. crassus* may be related to the movement and distribution of intermediate and paratenic hosts, which are believed to be the main

Table 2. *Anguillicola crassus*, *Anguilla rostrata*. Prevalence and intensity of *A. crassus* infection in eels *A. rostrata* collected within the commercial fishery from New Brunswick and northern Nova Scotia. The Prince Edward Island and Newfoundland eels were only available through swim bladder samples of eels collected from these provinces. All eels were ≥300 mm total length

River (Location)	Number of eels Collected	Infected	Prevalence (%)	Intensity
New Brunswick				
St. Johns River	28	1	3.6	1.0
Silver Lake (Amherst)	32	1	3.1	1.0
Nova Scotia				
Lochabere Lake (Antigonish)	27	4	14.8	2.5
Margaree Harbor (Cape Breton)	26	8	30.1	6.1
Bras d'Or Lake (Cape Breton)	28	4	14.3	4.0
Prince Edward Island				
Malpeque Bay (Northwest of Charlottetown)	146	0	0.0	0.0
Newfoundland				
Bonavista Bay (Southwest of Gander)	133	0	0.0	0.0

mechanisms behind the parasite's rapid dispersal in European eels considering the extensive range of both types of transitional hosts (Moravec 1992, Moravec & Skoríková 1998). Deep snout pipefish and black goby have been naturally infected with nematodes in the Baltic Sea, confirming freshwater, estuarine, and marine infections (Reimer et al. 1994). This supports the hypothesis that the parasite is not restricted to freshwater and can potentially be transferred to new locations through all salinity regimes and through many paratenic hosts (reviewed by Taraschewski 2006). The vast array of potential hosts and the eel's generalist feeding behavior (Helfman et al. 1987, Barak & Mason 1992) ensure that the parasite's distribution will not be limited by host availability. Yellow American eels exhibit homing, home site fidelity, and limited home ranges (Parker 1995, Oliveira 1997, Morrison & Secor 2003), and thus their movements are unlikely to contribute to the parasite's spread between river systems. It is also conceivable that the current distribution is related to anthropogenic mechanisms. Although natural eel movement may not enhance parasite spread between rivers, eels sold for live bait may do so. Live eels are transported between rivers as bait, primarily to supply recreational fisheries, potentially spreading the parasite to an entirely different river system from that in which the eel originated. In addition, 6 of the 8 areas with the highest prevalence and greatest intensity in the present study were in the vicinity of major shipping ports (Boston, Massachussetts, New Bedford, Massachussetts, and Portland, Maine). In a study of the exotic American eel gill parasites *Pseudodactylogyrus bini* and *P. anguillae*, it was hypothesized that they were introduced along with *A. crassus* through either commercial imports of foreign eels or by transmission through ballast water (Hayward et al. 2001). Machut & Limburg (2008) found increased infection rates in tributaries of the Hudson River that exhibited higher urbanization, indicating that anthropogenically induced eel susceptibility to the parasite may also be a factor involved in parasite distribution. The presence of the parasite in the St. Johns River can be explained by the natural advancing of the parasite along the coast from New England rivers. This collection was conducted 2 yr after the parasite had been found within the Penobscot River drainage approximately 180 km away. However, the presence of the parasite in northern New Brunswick and Nova Scotia, while being absent in the southern portion of Nova Scotia, is problematic and indicative of a secondary mode of transport.

The distribution of *Anguillicola crassus* found in the present study does not appear to be limited by temperature, as has been suggested in other studies (Knopf et al. 1998). Eels from the Penobscot River drainage are infected with *A. crassus*, and this system has similar annual water temperatures to the East Machias River, Maine, the northernmost site sampled within the USA, and to the southern Nova Scotia rivers. Knopf et al. (1998) proposed that American eels of the St. Lawrence River would not be affected by a northward expansion because low winter water temperatures would hinder the parasite's survival. They also state that L_3 stage larvae can withstand 4°C for periods up to 4 mo, with low temperature presumably causing delayed development and high mortality of the adult parasite phase within the eel. However, the parasite is well established in Penobscot River eels, which are subjected to mean water temperatures of <4°C for 4 mo yr^{-1} (US Geological Survey 2001). The presence of the parasite in northern Nova Scotia and New Brunswick does not support this temperature-limiting hypothesis either, and it is probable that the parasite will eventually be found further north, possibly entering the St. Lawrence River system, before temperature becomes an actual limiting factor.

As a panmictic species (Avise et al. 1986, Wirth & Bernatchez 2003), the spread of the parasite into more northern locations will only add to the eel's current recruitment problems. Further study of *Anguillicola crassus* is thus necessary to better understand the mechanisms determining its distribution and rate of dispersal, in order to assess the future effect of this parasite on the American eel.

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