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Anguillicola crassus infection in *Anguilla rostrata* from small tributaries of the Hudson River watershed, New York, USA

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ABSTRACT: We studied the invasion of the exotic nematode parasite *Anguillicola crassus* in the American eel *Anguilla rostrata* using tributaries of the Hudson River estuary. Yellow-phase American eels were sampled from 6 tributaries, and their swim bladders were examined for nematode infection. Prevalence averaged 39% with an intensity of 2.4 nematodes per eel. Parasite distribution was not significant along a latitudinal gradient; on the other hand, physical barriers (dams and natural waterfalls) significantly reduced infections upstream. Urbanization may increase the susceptibility of eels to infection; we found significantly elevated infection rates when urbanized lands exceeded 15% of the tributary catchment area. Yellow-phase eel condition was not affected by parasite infection. The invasion of the entire Hudson River watershed is ongoing and therefore will continue to be a management concern. Further analysis of the parasite–host interaction in North America is warranted.

KEY WORDS: *Anguilla rostrata* · *Anguillicola crassus* · Parasite · Barriers · Urbanization

INTRODUCTION

Considered an important commercial fish (ASMFC 2000, Tesch 2003), the decline in American eel *Anguilla rostrata* populations has been widely documented along the eastern coast of North America (Castonguay et al. 1994, Richkus & Whalen 1999, Haro et al. 2000). Coincident precipitous declines in anguillids worldwide (ICES 2004) have led to increased interest in the biology of the eel. One proposed component of this population reduction is the invasion of the exotic nematode swim bladder parasite *Anguillicola crassus* into European eel *Anguilla anguilla* and American eel stocks. As a relatively new host for the parasite, the American eel may be highly susceptible to infection.

Native to Asia, *Anguillicola crassus* was first reported in 1982 from wild and cultured European eel stocks (Peters & Hartmann 1986 and citations within), quickly spread, and achieved prevalence near 100% in some drainages (Kennedy & Fitch 1990, Kirk 2003). The invasion of *A. crassus* into North America was first documented in 1995 at Texas aquaculture facilities, and the parasite was subsequently collected from a single wild South Carolina eel (Fries & Williams 1996). Successive studies reported American eel stocks from Florida to New York infested with *A. crassus* (Barse & Secor 1999, Barse et al. 2001, Moser et al. 2001). Recently, the parasite was also collected in Massachusetts (K. Oliveira, University of Massachusetts Dartmouth, pers. comm.).

Proliferation of the nematode is facilitated by its high fecundity and short life cycle, completed in as little as 2 mo (De Charleroy et al. 1990), and an ability to survive varying salinities (Kennedy & Fitch 1990, Kirk et al. 2000). Paratenic hosts for *Anguillicola crassus* are diverse (Thomas & Ollevier 1992, Moravec & Skoríková 1998) and aided the spread of the parasite in Europe.

Eels, the definitive host for *Anguillicola crassus*, become infected when they ingest either intermediate or paratenic hosts (Moravec & Konecny 1994, Nimeth

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et al. 2000). Intense infections can cause hemorrhagic lesions of the swim bladder, swim bladder fibrosis, skin ulcers and swollen anuses (van Banning & Haenen 1990). There are contrasting findings regarding the potential negative affects of *A. crassus* on swimming ability (Sprengel & Lüchtenberg 1991, Nimeth et al. 2000, Münderle et al. 2004). Knopf et al. (1998) theorized that infestation of European eels may have been slowed by low water temperatures, and increased parasite intensity was found in thermal effluent when compared to cooler surrounding waters (Höglund et al. 1992b). Examination of American eel in Canadian waters has not yet shown infection with *A. crassus* (Marcogliese & Cone 1996, G. Verreault, Faune et Parcs Quebec, pers. comm.).

Within New York State the tidal Hudson River contains infected eels with prevalence increasing downstream (Morrison & Secor 2003). However, the rate of infection and infected eel condition in Hudson River tributaries is unknown. Densities of up to 1.55 eels m^{-2} have been found in the tributaries (Machut et al. 2007), suggesting that they are an important habitat for declining American eel populations. As a relatively new definitive host for the parasite, eels in the Hudson River tributaries may be highly susceptible to infection.

The purpose of the present study was to examine yellow-phase eels taken from small tributaries of the freshwater tidal Hudson River estuary to determine the burden of *Anguillicola crassus* on native American eel populations in these habitats, as well as the current effect of this parasite on the health of yellow-eels. We hypothesized that (1) the infection of eel with the *A. crassus* parasite would be higher in southern tributaries; (2) barriers would inhibit the upstream invasion of *A. crassus* in the tributaries; (3) disturbances caused by urbanization would increase the infection of American eels with *A. crassus*; and (4) eels infected with *A. crassus* would show a decreased health state when compared to uninfected eels.

MATERIALS AND METHODS

The Hudson River estuary is located in eastern New York State (Fig. 1), with over 100 tributaries ranging from first to sixth order below the federal dam at Troy, NY (river km, rkm, 252). Six tributaries of the Hudson River estuary were selected for sampling (Table 1): Wynants Kill, Hannacroix Creek, Black Creek, Saw Kill, Peekskill Hollow Brook and Minisceongo Creek. Streams estimated to have a large numbers of barriers were paired with streams estimated to have relatively few barriers along a north–south gradient from Troy, NY, to West Haverstraw, NY (rkm 58). Barriers were either natural waterfalls or manmade structures (mill dams or water control structures) of at least 0.5 m in height.

Location and selection of sampling sites were adjusted to maximize the inclusion of barriers and allow easy access. Streams were predominantly wadable from source to sink, and sampling was carried out in water <1 m in depth. Within each tributary 6 to 7 stream segments of ~50 m, selected at ca. even intervals from the mouth, were isolated using 5 mm diameter nylon mesh block nets and were electro-fished using a backpack shocker (Smith-Root, variable voltage) from June to August of 2003 and 2004. Eels were sedated with clove oil, counted and measured for total length and weight, and we noted any obvious swellings, lesions or ulcers. Of 1935 eels captured, 232 were collected in a size-stratified random sub-sample, euthanized and frozen for later dissection.

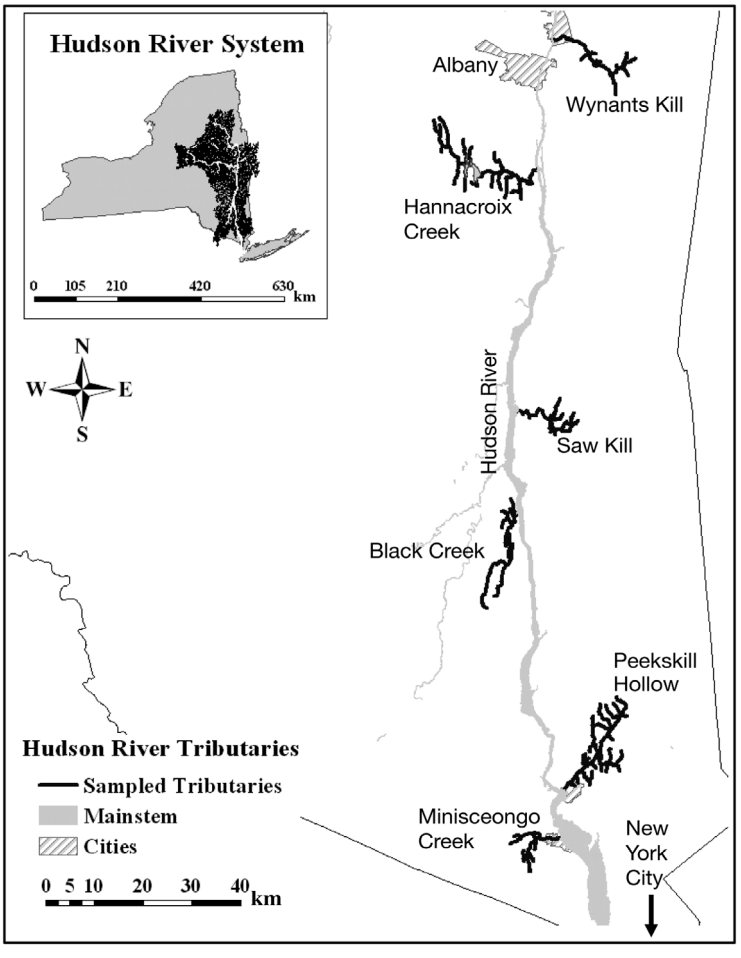

Fig. 1. Hudson River estuary including the 6 study tributaries. Map courtesy of D. McDonald, USGS, and L. Machut

Table 1. Watershed characteristics for study tributaries. % artificial barrier: proportion of all barriers on a tributary that are manmade (e.g. mill dams) within the zone of the present study

Tributary	Watershed area (km^2)	Distance (km) to Hudson mouth	Stream length (km)	No. of barriers	% artificial barrier	Avg. barrier height (m)
Wynants Kill	85.47	232.5	25.95	7	43	3.51
Hannacroix Creek	166.24	204.4	37.81	5	40	4.39
Saw Kill	66.29	153.8	22.62	7	43	3.27
Black Creek	87.77	132.4	29.55	9	22	2.47
Peekskill Hollow	135.51	69.2	28.11	4	100	1.81
Minisceongo Creek	47.90	58.0	18.85	6	100	2.51

In the lab swim bladders were removed, fixed in formalin and stored in 70% ethanol. We counted L3, L4 and adult-stage *Anguillicola crassus* nematodes in the swim bladder lumen and combined all stages for analysis. We tabulated prevalence (infected eels divided by total eels sampled), intensity (nematodes eel^{-1}) and mean abundance (total parasite no. divided by total eels collected) (Bush et al. 1997).

American eels were grouped for analysis by sample site and stream in order to examine the impact of a north–south gradient, barriers, and urbanization pressure on the intensity of infection of the *Anguillicola crassus* nematode. We grouped sample sites into 2 barrier classes: sampling locations below and above the second stream barrier. Tributaries were also classed as having low versus high urbanization pressures based upon GAP analysis of land-cover types (http://gapanalysis.nbii.gov) for the 6 tributary watersheds using ArcMap GIS software, version 8.2 (ESRI). Analysis of variance (ANOVA) was used to classify tributaries as urbanized or not (based on a threshold of 15% urbanization of the catchment). Degree of urbanization of the surrounding watershed was then tested as a factor in the distribution of the parasite. Stepwise linear regressions were performed to determine significant relationships between mean parasite abundance in American eels and the following factors: (1) the number of barriers between a sampling site and the confluence of the tributary with the Hudson River; (2) the distance of the sampling site from the mouth of the tributary; (3) sampling site eel density as determined by the Binomial depletion model (Machut et al. 2007); (4) the proportion of channel urbanization at the sampling site; (5) the proportion of riparian urbanization at the sampling site; (6) the proportion of riparian urbanization upstream of the sampling location; (7) the proportion of sub-catchment urbanization (as determined by ArcMap) for the sampling site; and (8) the proportion of urbanization within the entire watershed above the sampling site. Effects of a north–south tributary gradient, barrier impact, and urbanization were individually tested using multivariate analysis of variance (MANOVA) comparisons between non-infected and infected eels. Although statistical analysis of percentages may be heteroscedastic (Zar 1984), arc-sin transformation to normalize our data did not significantly alter statistical significance or conclusions; therefore, for ease of interpretation, we reported the raw data.

External comparisons were also made between non-infected and infected eels using an eel condition factor. Whereas some have used histological measurements to determine the effect of *Anguillicola crassus* on the health of eel (Höglund et al. 1992a, Kelly et al. 2000), we developed a condition factor as a proxy for health, as have others (e.g. Moser et al. 2001). Eel condition factor was calculated by determining predicted weights through nonlinear regression using observed total lengths and wet weights ($W = a \times L^b$). Standardized residuals were calculated (Sokal & Rohlf 1995) as a measure of relative eel condition, regressed by eel total length, and compared using ANCOVA.

An alpha level of 0.05 was used as the critical value to determine statistical significance. All statistical analyses were performed using STATISTICA, version 6.0 (StatSoft).

RESULTS

Eels analyzed in the lab ranged in total length from 58 to 710 mm (mean = 259 mm, median 236 mm); those infected with *Anguillicola crassus* ranged from 70 to 692 mm (mean = 271 mm, median = 265 mm). Visual inspection of the swim bladder lumen ranged from empty, non-infected tissue to *A. crassus* nematodes fully occupying distended swim bladders. One pale and sluggish eel with ulcers was captured in the Minisceongo Creek and died before immersion in clove oil. When dissected, its swim bladder hemorrhaged when touched and was greatly distended in relation to swim bladders of healthy eels of similar size. The individual had 4 adult nematodes filling the lumen, which was also filled with blood. While a few eels in the Wynants Kill suffered ulcers and inflamed anuses, not all were associated with *A. crassus* infection.

Mean prevalence of *Anguillicola crassus* in Hudson River tributary yellow-phase eels was 39%, range 32 to 52% (Table 2). Highest prevalence was found in Wynants Kill, while the lowest prevalence was found in Black Creek. Prevalence at each sampling location ranged from 0 to 63%. Mean intensity was 2.4 nematodes per infected eel, range 1.6 to 2.7. Saw Kill had the lowest intensity of *A. crassus* infection, while the highest intensity was found in Peekskill Hollow Brook. Individual American eel intensity of infection ranged from 0 (uninfected) to 20 nematodes eel^{-1} (Fig. 2). Intensity was not related to total eel length ($p = 0.61$). Due to the high degree of variation in intensity and prevalence among sites, infection rates were not correlated with the north–south gradient ($p = 0.67$). High prevalence and intensity were found in the northernmost tributary (Wynants Kill) as well as the southernmost tributaries (Peekskill Hollow Brook and Minisceongo Creek); lower prevalence and intensity were found in a northern tributary (Hannacroix Creek) and in the central tributaries (Saw Kill and Black Creek).

Stepwise linear regression produced a best fit estimate for *Anguillicola crassus* mean abundance as:

$$\text{Mean abundance} = 0.777 - (0.157 \times \text{Barriers}) + (0.687 \times \text{SC\_URB})$$
$$(r^2 = 0.48, p < 0.001)$$

Table 2. *Anguillicola crassus* infections of Hudson River tributary eels, by distance upstream from the Hudson River confluence and number of barriers traversed

Tributary	Distance (km)	No. of barriers	No. of eels	Prevalence (%)	Mean intensity	Mean abundance
Wynants Kill	0.39	1	10	60.0	2.67	1.60
	0.71	2	10	60.0	2.33	1.40
	0.94	4	0	0.0	0.00	0.00
	1.17	6	6	33.3	1.50	0.50
	3.58	7	1	0.0	0.00	0.00
	Total		27	51.9	2.36	1.19
Hannacroix Creek	0.74	0	16	43.8	3.43	1.50
	1.96	0	12	50.0	1.67	0.83
	4.00	1	3	33.3	1.00	0.33
	13.72	3	5	0.0	0.00	0.00
	17.91	3	6	16.7	4.00	0.67
	Total		42	35.7	2.60	0.90
Saw Kill	0.23	0	16	43.8	2.00	0.88
	0.34	1	9	33.3	1.00	0.33
	0.49	2	0	0.0	0.00	0.00
	1.23	5	3	0.0	0.00	0.00
	5.72	6	1	0.0	0.00	0.00
	Total		29	34.5	1.70	0.55
Black Creek	0.35	0	15	40.0	2.67	1.07
	1.19	0	16	37.5	1.83	0.69
	3.23	4	2	0.0	0.00	0.00
	3.33	4	0	0.0	0.00	0.00
	11.16	9	5	0.0	0.00	0.00
	Total		38	31.6	2.25	0.66
Peekskill Hollow Brook	3.69	0	16	50.0	2.88	1.44
	4.32	1	9	55.6	3.60	2.00
	7.69	1	10	30.0	1.33	0.40
	9.35	2	1	0.0	0.00	0.00
	11.90	2	2	50.0	2.00	1.00
	17.03	2	1	0.0	0.00	0.00
	Total		39	43.6	2.76	1.27
Minisceongo Creek	0.73	0	16	43.8	4.14	1.81
	1.88	0	16	50.0	2.38	1.19
	2.35	1	13	53.8	1.29	0.69
	3.25	2	10	10.0	2.00	0.20
	5.75	4	0	0.0	0.00	0.00
	5.81	4	2	0.0	0.00	0.00
	Total		57	40.4	2.57	1.18
All streams			232	39.2	2.44	0.93

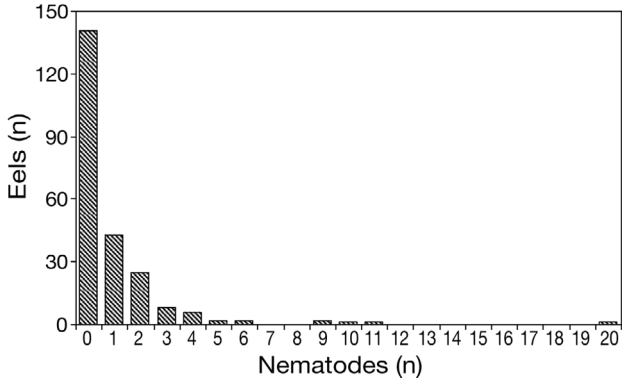

Fig. 2. *Anguillicola crassus* distribution in the *Anguilla rostrata* swim bladder

where barriers are the number of barriers between the sampling site and the confluence of the tributary with the Hudson River mainstem, and 'SC_URB' denotes the proportion of the sampling site's sub-catchment that is urbanized. Both variables were significant ($p < 0.05$), while all other factors were deemed insignificant (F to enter = 0.10) by stepwise linear regression.

Both mean prevalence and intensity were reduced as barrier numbers increased (Fig. 3). Whereas distance upstream from the mouth of the tributary had little effect on parasitic infection parameters ($p = 0.47$), MANOVA suggested that *Anguillicola crassus* prevalence and intensity decreased significantly beyond the second barrier ($p < 0.01$). Increased *A. crassus* prevalence and intensity in stream sections above the fifth barrier were attributed to one sampling location within Wynants Kill, a highly urbanized stream with high prevalence overall. One eel, 116 mm total length, was found above the third barrier of Hannacroix Creek infected with 4 nematodes; this single eel accounted for the entire prevalence and intensity in sites located beyond the third barrier. No other sites had infected eels above the second barrier. Thus, invasion of *A. crassus* within the small tributaries of the Hudson River watershed may have been ongoing during sampling.

ANOVA indicated that 3 tributaries (Wynants Kill, Minisceongo Creek, and Peekskill Hollow Brook) had significantly higher percent urbanized land-cover, greater than 15%, within the watershed than less urbanized tributaries (Saw Kill, Hannacroix Creek, and Black Creek; $p = 0.03$). These latter streams were less than 10% urbanized (Fig. 4) and were dominated, greater than 66%, by forested land-cover. Although higher nematode abundances were found in urbanized sites, this was not significant ($p = 0.14$). Dissected eels within the urbanized watersheds of Wynants Kill, Peekskill Hollow Brook, and Minisceongo Creek also showed infection with other fish parasites (such as *Eustrongylides*) not commonly found within non-urbanized watersheds.

Eel relative condition factor was not significantly related either to nematode prevalence or intensity ($p = 0.47$ both), suggesting yellow-phase eels infected with *Anguillicola crassus* had, by this metric, health similar to non-infected eels while residing in the tributaries (Fig. 5). Mortality from infection could not be measured accurately in the field. No other health diagnostics were performed.

DISCUSSION

Mean intensities of *Anguillicola crassus* infection for the 6 tributaries studied, and infection intensities for individual eels, were lower than those found in studies of the main channel of the Hudson River, Chesapeake Bay tributaries, and South Carolina streams (Barse et al. 2001, Moser et al. 2001, Morrison & Secor 2003). Individual intensities of >50 were recorded within these systems, compared to the present study's highest

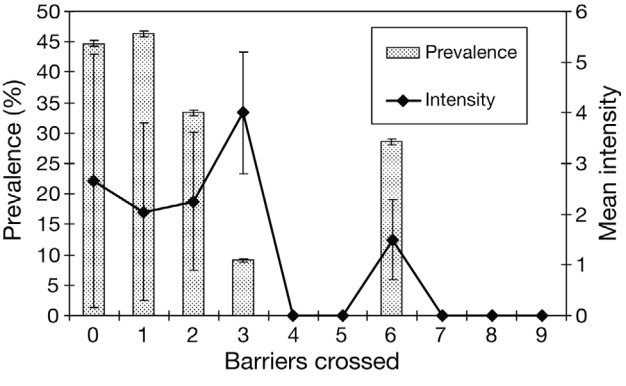

Fig. 3. *Anguillicola crassus* infecting *Anguilla rostrata*. Mean (±1 SD) prevalence and intensity in relation to the number of barriers between tributary mouth and collection location

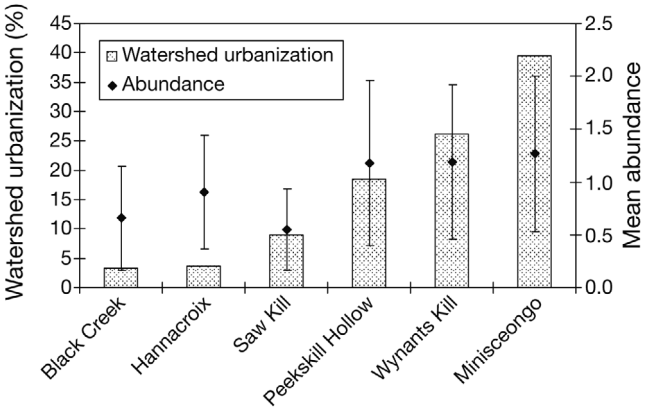

Fig. 4. *Anguillicola crassus* mean (±1 SD) abundance in *Anguilla rostrata* (◆) and percent urbanization of respective tributaries (bars)

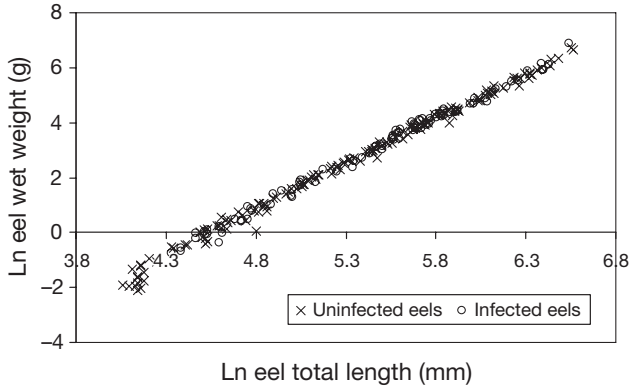

Fig. 5. *Anguilla rostrata* relative condition determined by standardized residuals of eel weight

intensity found in a single eel with 20 nematodes collected near the mouth of Minisceongo Creek. Mean *A. crassus* prevalence was also higher in other studies than within the 6 Hudson River tributaries. We found a greater size range of infected American eels than previously reported (cf. ≥105 mm, Moser et al. 2001, or ≥200 mm, Barse et al. 2001, Morrison & Secor 2003). Intensity of infection was not related to eel total length in the present study. Parasite pressure in the Hudson River tributaries appears to be lower than found in larger river systems. We will address several factors that may produce this lower distribution and intensity of *A. crassus* in Hudson River tributaries.

Low winter water temperatures may reduce the impact of *Anguillicola crassus* (Knopf et al. 1998) and may be a partial cause for the lower prevalence and intensities in Hudson River tributaries than found in the mainstem. Small tributaries, with lower discharge rates, respond more strongly to atmospheric cooling throughout the year than do larger tributaries or the main river channel. Therefore, lower water temperatures may be found in small tributaries during winter, which negatively impact the life cycle of *A. crassus* (Nagasawa et al. 1994). Although water temperature may slow invasion, this does not mean invasion will not occur. In a laboratory experiment Knopf et al. (1998) found increased nematode mortality and a failure of L3 *A. crassus* larvae to invade the swim bladder wall at 4°C compared to warmer water treatments. However, it was noted that once temperatures were raised to 18°C, the nematode was able to continue its life cycle and complete the invasion. Therefore, although parasite infection may be slow, it will still occur and spread in range. The parasite has been documented as far north as Maine freshwaters (Aieta 2006), and the northern extent of the parasite's range in North America is uncertain. Further study of the effect of extreme cold water temperatures, below 4°C, is warranted.

Given the high fecundity of *Anguillicola crassus* (De Charleroy et al. 1990) and the presence of the nematode in the mainstem of the Hudson River for several years (Barse & Secor 1999), the lack of significance of a north–south gradient is reasonable. Glass eels entering the system are infected when feeding upon parasite host copepods (Nimeth et al. 2000) or paratenic hosts (Thomas & Ollevier 1992, Moravec & Konecny 1994, Moravec & Skoríková 1998) as they migrate upstream to nursery habitats.

Little work has been done to document fish parasite invasion in relation to barriers, including in American eels. In some systems barriers have been shown to alter parasite distribution (Bauer & Stolyarov 1958, Hla Bu & Seng 1997, Barger & Esch 2001). For *Anguillicola crassus* in Hudson River tributaries, barriers are slowing, but not eliminating, the invasion of *A. crassus,* which is self-sustaining in an area once colonized. We suggest that barriers currently play the most important role in determining the presence and distribution of the *A. crassus* parasite in American eel in Hudson River tributaries. Eel density was not a significant variable in modeling mean parasite abundance in sampling sites, and parasite intensity is higher within mainstem eel populations, although densities are lower than found in censused tributaries (Morrison & Secor 2003, Machut et al. 2007). Barger & Esch (2001) suggested that breaks in parasite distribution due to natural and manmade barriers were caused by breaks in the distribution of potential host species. An important difference between *A. crassus* transport throughout barrier-impacted watersheds from that of other parasites and from other systems is its dependence upon American eel migration. Although other hosts, such as frogs, may be able to circumvent barriers, the rate at which this may occur is unknown. Other potential paratenic hosts, such as other fishes, are unlikely to be able to scale barriers in this system. Thus, limitations of American eel movement over barriers may primarily regulate parasite diffusion.

At the time of this study (2003 to 2004) eels within the upper reaches of the tributaries were experiencing low parasite pressure. Eels are found to migrate upstream until reaching total lengths of ~250 mm (Haro & Krueger 1991, Oliveira 1997). Sampling locations in the upper reaches of the tributaries consisted almost exclusively of older, larger females (>400 mm total length) that had migrated into the streams before the parasite invasion. Predominantly, only large females are found beyond the second barrier (Machut et al. 2007). Given the high susceptibility of American eel to infection from *Anguillicola crassus*, low prevalence in the upper streams can only be supported if propagule pressure is low. Migration of small eels upstream, as in the case of a single small eel found at a

Hannacroix Creek site ~17 km upstream from the confluence with the Hudson River, may provide the propagules for further nematode infection and establishment of resident parasite populations. That individual measured 221 mm and moved upstream, from lower sections of the tributary where *A. crassus* was prevalent, over 2 natural falls of 3.5 and 8.5 m, respectively, and a 1.4 m water-supply dam. We propose that as young, infected eels migrate over barriers, invasion of previously healthy systems will occur and that this is the predominant invasion pathway for tributaries with numerous barriers. Older females residing behind several barriers have low probability of coming into contact with infected eels, and it will take several years for infected eels to move sufficiently far upstream to release L2 stage larvae.

The trend toward higher infection of American eel with *Anguillicola crassus* in urbanized watersheds suggests that urbanization may increase eel susceptibility to infection by increasing stressors. The low number of urban sites in the present study, and consequently low statistical power, may have limited our ability to distinguish significant effects, but the trends are in accordance with other studies. Urbanization of landscapes has been linked to increased parasite infection in other systems (Friesen & Ward 1996, Coyner et al. 2002), and secondary infections may become increasingly prevalent in stressed eels (van Banning & Haenen 1990). Therefore, given these additive stresses upon the eel, including several other gut parasites, it is not surprising to find that these eels had the highest extent of *A. crassus* infection when compared to the remaining streams.

Given the high prevalence and intensity of *Anguillicola crassus* infection in anguillid eels (Kennedy & Fitch 1990, Kirk 2003), urbanization pressures may increase the initial susceptibility of American eels and shorten the time period for invasion/establishment of a local parasite community. Thus, while *A. crassus* infection may be inevitable for American eels in Hudson River tributaries, the rate and intensity of infection may be related to urbanization of the surrounding landscape. Further examination of urbanization pressures and mechanisms on the infection of American eel with *A. crassus* is also warranted.

Paratenic hosts in North America have not yet been identified, although a wide range of European paratenic hosts for *Anguillicola crassus* have been documented including (1) aquatic vertebrates such as frogs and newts (Moravec & Skoríková 1998); (2) common stream fish such as trout, perch and sunfish (van Banning & Haenen 1990, Thomas & Ollevier 1992, Moravec & Konecny 1994); and (3) aquatic invertebrates such as Megaloptera, Odonata and Trichoptera (Moravec & Skoríková 1998). Although similar (e.g. sister) species may be found in the Hudson River watershed, differences among species may result in different probabilities of the North American species becoming a paratenic host. While unknown, potential variance in paratenic host communities between tributaries and the main stem, large tributaries and small tributaries, as well as differences between upstream and downstream segments of tributaries, may be important in determining hosts (e.g. Barger & Esch 2001, Thorp & Covich 2001). Increased urbanization may also alter the distribution of paratenic hosts. Paratenic hosts for *A. crassus*, and their distribution, should therefore be identified in North America.

As in other studies (Kelly et al. 2000, Moser et al. 2001), we found no evidence that yellow-phase eel health is currently altered by the presence of *Anguillicola crassus*. While there are noted histological changes upon infection (Höglund et al. 1992a, Molnár 1994), eel health as determined by ANCOVA of length–weight relationships to infection (the present study), gut fullness (Moser et al. 2001), and metabolic status (Kelly et al. 2000) suggest that yellow-phase eels appear to acclimate to chronic infection. Infection with *A. crassus* does not affect the swimming ability of the immature eel (Nimeth et al. 2000, Münderle et al. 2004); thus, prey acquisition and predator avoidance should not be adversely affected. However, it has been suggested that infestation with *A. crassus* may alter the ability of migrating eels to undergo daily vertical migrations and successfully complete migration to the Sargasso Sea (Kirk et al. 2000). During freshwater residency multiple stressors may be present in the natural environment at any given time, enhancing the negative effect of *A. crassus* infection. Pathological changes and the rate of American eel natural mortality due to *A. crassus* has not been studied; only assumptions based upon pathological changes in European eel (van Banning & Haenen 1990, Kirk et al. 2000, Würtz & Taraschewski 2000) can be made.

Given that we believe the invasion of the tributaries is still ongoing, future examination of these tributaries should be made to catalogue the continued spread of the invasion, the intensity of infection and the impact of watershed urbanization. Further studies in New England and Canadian provinces would be helpful to determine the potential northern extent of *Anguillicola crassus* invasion.

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