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THE SWIMBLADDER NEMATODE *ANGUILLICOLA CRASSUS* IN AMERICAN EELS (*ANGUILLA ROSTRATA*) FROM MIDDLE AND UPPER REGIONS OF CHESAPEAKE BAY

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ABSTRACT: The patterns of infection of American eels *Anguilla rostrata*, with the introduced swimbladder nematode *Anguillicola crassus*, in tributaries of middle and upper Chesapeake Bay are described. A total of 423 subadult eels was collected from 8 Bay tributaries from spring 1998 to fall 1999. Also, 30 elvers were collected from Ocean City, Maryland, in spring 1998. The numbers of juvenile and adult specimens of *A. crassus* in the swimbladder wall and lumen were counted. No elvers were infected. In subadult eels, prevalence of adult and juvenile stages combined ranged from 13% to 82%; mean intensity ranged from 2.6 to 9.0 worms per eel. Infection levels were highest for Susquehanna River eels (northernmost river) and lowest in the southernmost sites: St. Jerome's Creek and the Pocomoke River. Although eels from these 2 localities were larger, the low infection rates there are most likely due to reduced transmission in higher salinity water and not to eel size. Eels with both adult and juvenile stages of *A. crassus* were more common than expected by chance. This might be explained by inhibition of juveniles migrating into the swimbladder lumen when adults are already present there.

The American eel *Anguilla rostrata* is found in brackish and saltwater marshes and in freshwater tributaries of the Atlantic Ocean from Greenland and Iceland to Venezuela (Helfman et al., 1987). Of the 15 species of anguillid eels, only the American eel occurs in North America. The life cycle of *A. rostrata* begins with leptocephalus larvae, which drift in the sea for about 1 yr, followed by transparent glass eels that enter the estuary and become pigmented elvers. Elvers either stay in the estuary or migrate upstream, and in either case, they metamorphose to yellow eels, an immature stage that lasts from 5 to 20 yr. Lastly, sexually mature silver eels migrate to the Sargasso Sea to spawn and then die (Helfman et al., 1987).

Anguillicola crassus is native to the Japanese eel (*Anguilla japonica*) in east Asian waters (Moravec and Taraschewski, 1988). This parasite was first documented in wild European eels *Anguilla anguilla* in Germany in 1982, and in the last 2 decades it has spread throughout Europe (Kennedy and Fitch, 1990; Moravec, 1992; Evans and Matthews, 1999). *Anguillicola crassus* was first documented in American eel (*A. rostrata*) populations in North America in 1995 (Fries et al., 1996).

All life stages of eels can become infected by consuming infected intermediate or paratenic hosts (De Charleroy et al., 1990; Thomas and Ollevier, 1992). Although only 3 definitive host species are known, numerous crustaceans, mostly copepods, can serve as the required intermediate host, and numerous species of fishes as well as snails, amphibians, and insect larvae can serve as a paratenic host (Moravec and Konecny, 1994; Moravec, 1996, Moravec and Škoríková, 1998). Intermediate or paratenic host species in North America have not been identified.

Prevalence of *A. crassus* in eels from 4 Chesapeake Bay tributaries ranged from 10 to 29% in 1997 (Barse and Secor 1999). The purpose of the present study was to elucidate further the patterns of infection in a larger portion of upper and mid-Bay localities for spring and fall 1998 and 1999. The specific objectives were (1) to look at the seasonal and spatial variation of infection in Chesapeake Bay, (2) to assess the relationship between infection rate and eel length, and (3) to determine if the presence of adult and juvenile stages of *A. crassus* was independent within individual hosts.

MATERIALS AND METHODS

A total of 423 American eels was collected in 4 seasonal samples from spring 1998 to fall 1999 from the middle and upper Chesapeake Bay (Table I; Fig. 1). Also, 30 elvers were collected in spring 1998 from Turville Creek, along the Atlantic coast in Ocean City, Maryland (Table I; Fig. 1). Eels were killed with tricaine methanesulfonate, weighed to the nearest gram, measured (total length) to the nearest millimeter, and frozen until necropsy. In the laboratory, swimbladders were excised and examined for the presence of adult *A. crassus*. Adults were counted, and a subsample was cleared in glycerol for species identification (Moravec and Taraschewski, 1988). Opened swimbladders were then pressed between 2 glass plates and examined for the presence of juvenile *A. crassus* using a dissecting microscope at ×25 magnification. The number of juveniles in each eel was recorded.

Data were analyzed using StatView 5.0 (SAS, 1998), and null hypotheses were rejected at $P < 0.05$. Parasitological terms follow those presented by Bush et al. (1997). Intensity of infection represents the total number of nematodes in individual hosts. Mean intensity is the average number of nematodes per infected host in a sample of hosts.

Prevalence and mean intensity of infection with *A. crassus* were calculated for adults, juveniles, and adults and juveniles combined for each sample of eels. Analyses of these data were limited to the combined numbers of adults and juveniles. The null hypothesis that prevalence and intensity of *A. crassus* were independent of locality within each season was tested. The null hypothesis that there was no difference in prevalence or intensity between years in the Susquehanna, Wye, and Wicomico rivers was also tested. Contingency table analyses were used to compare prevalence data, and deviations of observed from expected frequencies were tested using chi-square tests of independence (Sokal and Rohlf, 1981). Intensity data were not normally distributed; therefore, Kruskal–Wallis or Mann–Whitney *U*-tests were used to compare intensity data, and Games/Howell tests were used to compare intensity data among localities (SAS, 1998).

The relationship between eel length and intensity of infection with *A. crassus* is illustrated with a scatterplot. Mean host length is presented for each seasonal sample. No further analyses of this relationship were done because the number of eels examined among samples was not equal and because eel length classes were not evenly distributed among samples.

A contingency table analysis was done to test the null hypothesis that the presence of adult and juvenile *A. crassus* were independent within host individuals. Eels were enumerated in 4 categories of infection: uninfected, infected with only juveniles, infected with only adults, and infected with both adults and juveniles. Observed and expected frequencies were compared with a chi-square test of independence.

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TABLE I. Number of eels, *Anguilla rostrata,* collected from 8 Chesapeake Bay localities and 1 locality in Ocean City, Maryland, in 4 seasonal samples.

	Season			
	1998		1999	
Locality	Spring	Fall	Spring	Fall
Chesapeake Bay				
Susquehanna River*	51	—	30	—
Sassafras River*	60	—	—	—
Chester River*	56	—	—	—
St. Jerome's Creek*	35	—	—	—
Wicomico River*	—	61	—	27
Wye River*	—	30	—	19
Eastern Neck Island*	—	—	31	—
Pocomoke River†	—	—	—	23
Ocean City				
Turville Creek‡	30	—	—	—

* Eel pot sampling method.
† Pound net sampling method.
‡ Elver trap sampling method.

RESULTS

Elvers examined from Ocean City were not infected with *A. crassus*. Mean prevalence of *A. crassus* for Chesapeake Bay yellow American eels was 40.2% for juvenile nematodes and 46.1% for adult nematodes (Table II). Mean intensity ranged from 1.8 to 6.2 juvenile worms and from 1.6 to 5.6 adult worms (Table II). Prevalence, mean intensity, and maximum intensity of infection of juvenile and adult stages of this parasite were highest in the spring 1998 Susquehanna River sample (Table II).

With adult and juvenile stages combined, prevalence of *A. crassus* ranged from 13 to 82%, mean intensity of infection ranged from 2.6 to 9.0 worms/eel, and maximum intensity of infection was 52 worms (Table III). Prevalence was not significantly different among localities during spring 1998 ($\chi^2 = 6.7$; $P > 0.05$), fall 1998 ($\chi^2 = 0.03$; $P > 0.50$), or spring 1999 ($\chi^2 = 2.0$; $P > 0.10$). Prevalence was significantly different among localities during fall 1999 ($\chi^2 = 26.6$; $P < 0.001$). There was no significant difference in prevalence between fall 1998 and fall 1999 in the Wicomico River ($\chi^2 = 2.5$; $P > 0.1$) or in the Wye River ($\chi^2 = 0.03$; $P > 0.5$). Prevalence was significantly higher in the Susquehanna River during spring 1998 compared with spring 1999 ($\chi^2 = 9.48$; $P < 0.005$).

There was no significant difference in intensity of *A. crassus* infections in fall 1998 ($U = 220.0$; $P > 0.6$) or fall 1999 ($H = 0.098$; $P > 0.9$) seasonal samples. Intensity of infection was significantly different among localities in spring 1998 ($H = 17.3$; $P < 0.001$). Pairwise comparisons revealed that Susquehanna River eels had significantly greater numbers of worms than eels from St. Jerome's Creek ($P < 0.05$), and eels from the Sassafras River also had greater numbers of worms than those from St. Jerome's Creek ($P < 0.05$). In spring 1999, intensity of infection was significantly higher for eels from the Susquehanna River than for those from Eastern Neck Island ($U = 80.0$; $P = 0.01$). Comparisons between years revealed no difference in intensity of infection for Susquehanna River eels from spring 1998 to spring 1999 ($U = 264.5$; $P > 0.3$), Wicomico River eels from fall 1998 to fall 1999 ($U = 297.0$; $P > 0.8$), or Wye River eels from fall 1998 to fall 1999 ($U = 71.5$; $P > 0.8$).

A scatterplot showed that little of the variation in intensity of infection can be explained by eel length (Fig. 2). Table III shows that eels of different lengths were not evenly distributed among seasonal samples. The largest eels were in the most southern sample localities.

The number of eels in 4 categories of infection were (1) 104 infected with both adult and juvenile stages of *A.crassus*, (2) 66 infected with only juvenile worms, (3) 91 infected with only adult worms, and (4) 162 uninfected. A contingency table analysis showed that there were more eels that were either infected with both adult and juvenile stages (category 1) or uninfected (category 4) than expected by chance, and there were too few eels infected with either juveniles only or adults only (categories 2 and 3) than expected by chance ($\chi^2 = 26.0$; $P < 0.001$). (These results were the same when data were analyzed by season.)

DISCUSSION

Reports of *A. crassus* infections of European eels are numerous; however, the present study is only 1 of a few recent reports of *A. crassus* infections in American eels in North America (Fries et al. 1996; Barse and Secor, 1999). It appears that *A. crassus* has successfully colonized eel populations in much of eastern North America from Florida (T. Harmon and R. Overstreet, pers. comm.), South Carolina (Fries et. al, 1996), North Carolina (M. Moser, pers. comm.), and Maryland and New York (Barse and Secor 1999), yet it has not been found in the St. Lawrence River (J. Dembeck, pers. comm.) or in Nova Scotia (Cone et al., 1993; Marcogliese and Cone, 1996) (Fig. 1). This supports the prediction of Knopf et al., (1998), that *A. crassus* will not invade eel populations in the St. Lawrence River or northward because of cold winter temperatures. Further surveys are needed to document range expansion of this potentially harmful parasite.

Barse and Secor (1999) and the present study document 10 middle or upper Chesapeake Bay localities where *A. crassus* is established (Fig. 1). Prevalence, intensity, or both were lowest in the 2 mid-Bay samples with the closest proximity to the Atlantic Ocean (i.e., the Pocomoke River and St. Jerome's Creek). Eels from these tributaries were larger than other eels examined (Table III), suggesting a possible negative correlation between eel size and infection rates. However, a scatterplot (Fig. 2) shows little correlation between these 2 variables. In Europe, researchers found high prevalence and intensity of *A. crassus* infections among all size classes of eels (De Charleroy et al., 1990; Thomas and Ollevier, 1992). Thus, host size is not a likely determinant of *A. crassus* infection levels.

Laboratory findings have confirmed that transmission does occur in brackish water because *A. crassus* can utilize the calanoid copepod *Eurytemora affinis*, a dominant species in tidal estuaries in the northern hemisphere, as intermediate host (Kirk, Kennedy, and Lewis, 2000). Marine fish paratenic hosts have also been identified in brackish waters (7–12°/∞) of the Baltic Sea (i.e., the black goby *Gobius niger* and the deep-snouted pipefish *Syngnathus typhle*) (Höglund and Thomas, 1992; Rei-

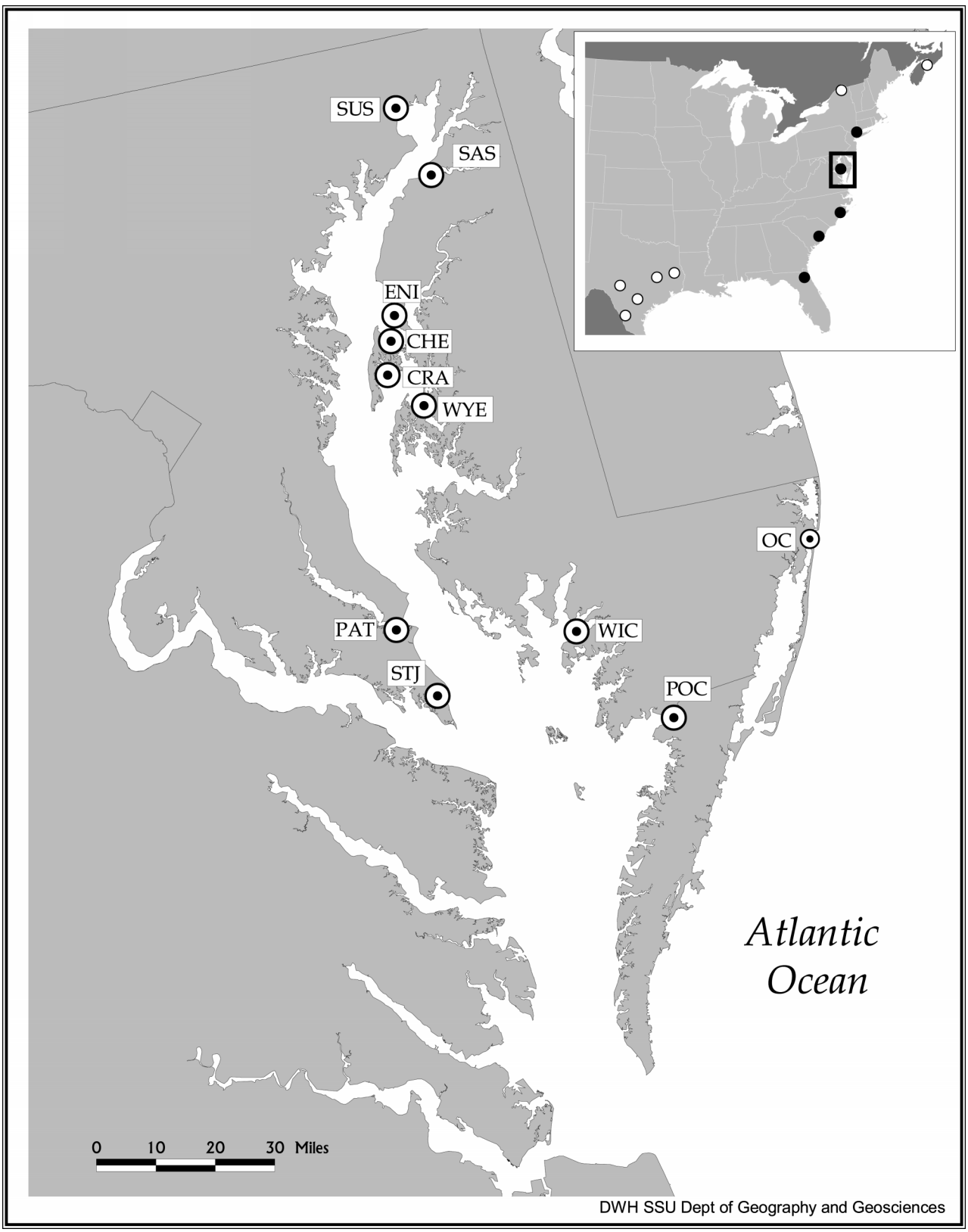

FIGURE 1. Map of Chesapeake Bay showing the localities where eels were collected for the present study (SUS, Susquehanna River; SAS, Sassafras River; CHE, Chester River; STJ, St. Jerome's Creek; WIC, Wicomico River; WYE, Wye River; ENI, Eastern Neck Island; POC, Pocomoke River; OC, Turville Creek, Ocean City, Maryland) and 2 additional localities sampled by Barse and Secor (1999) (CRA, Crab Alley Bay; PAT, Patuxent River) that were not studied again here. Inset: Map of eastern North America showing localities where American eels *Anguilla rostrata* have been examined for the presence or absence of *Anguillicola crassus*. Open circles, absent; closed circles, present.

TABLE II. Prevalence (P), mean intensity and standard error (SE) of infection, and maximum (Max) intensity of infection with adult and juvenile stages of *Anguillicola crassus* in American eels (*Anguilla rostrata*) from Chesapeake Bay.

	Juvenile			Adult		
Sample*	P	Mean (SE)	Max	P	Mean (SE)	Max
SUS SP98	58.8	6.2 (1.3)	34	70.6	5.3 (0.9)	23
SAS SP98	56.7	4.3 (0.6)	17	46.7	3.4 (0.6)	14
CHE SP98	33.9	1.8 (0.3)	6	53.6	3.9 (0.6)	13
STJ SP98	57.1	2.4 (0.4)	6	40.0	1.6 (0.3)	4
WIC F98	29.5	4.0 (0.8)	13	37.7	2.8 (0.5)	10
WYE F98	26.7	2.1 (0.4)	4	36.7	2.7 (0.5)	5
ENI SP99	41.9	2.3 (0.5)	6	48.4	2.3 (0.5)	9
SUS SP99	33.3	2.5 (0.6)	7	43.3	3.6 (0.5)	7
WIC F99	48.1	3.6 (1.2)	17	44.4	4.4 (1.4)	17
WYE F99	21.1	2.3 (0.8)	4	52.6	3.4 (1.0)	11
POC F99	4.3	2.0 (—)	2	13.0	2.0 (0.6)	3
All eels	40.2	3.6 (0.3)	34	46.1	3.6 (0.3)	23

* SUS, Susquehanna River; SAS, Sassafras River; CHE, Chester River; STJ, St. Jerome's Creek; WIC, Wicomico River; WYE, Wye River; ENI, Eastern Neck Island; POC, Pocomoke River; SP, spring; F, fall.

TABLE III. Mean host length, prevalence of infection, and mean and maximum intensity of infection with *Anguillicola crassus* (adult and juvenile stages combined) in 11 seasonal samples of eels (*Anguilla rostrata*).

			Intensity	
Sample*	Mean length (SE) (cm)	Prevalence	Mean (SE)	Maximum
SUS SP98	35.4 (1.5)	82.4	9.0 (1.6)	52
SAS SP98	32.2 (1.4)	71.7	5.6 (0.8)	19
CHE SP98	33.9 (1.2)	60.7	3.9 (0.7)	15
STJ SP98	46.2 (1.3)	77.1	2.6 (0.4)	8
WIC F98	36.1 (1.5)	52.5	4.3 (0.8)	23
WYE F98	34.6 (1.0)	50.0	3.1 (0.5)	7
ENI SP99	36.5 (1.7)	67.7	3.3 (0.7)	13
SUS SP99	28.4 (1.5)	50.0	4.8 (0.6)	11
WIC F99	40.2 (1.7)	70.4	5.3 (1.4)	22
WYE F99	42.4 (2.3)	52.6	4.3 (1.5)	14
POC F99	62.5 (1.6)	13.0	2.7 (0.3)	3
All eels	37.1 (0.6)	61.7	50 (0.4)	52

* SUS, Susquehanna River; SAS, Sassafras River; CHE, Chester River; STJ, St. Jerome's Creek; WIC, Wicomico River; WYE, Wye River; ENI, Eastern Neck Island; POC, Pocomoke River; SP, spring; F, fall.

mer et al., 1994). However, high salinity can inhibit *A. crassus* life cycle completion (Kirk, Kennedy, and Lewis, 2000; Kirk, Lewis, and Kennedy, 2000). Therefore, lower levels of infection are expected in southern and more saline regions of Chesapeake Bay.

In the Sassafras River, prevalence of adult *A. crassus* doubled from spring 1997 to spring 1998 (24 to 47%; Barse and Secor, 1999; Table II), whereas mean intensity of infection has remained about the same (3.1 vs. 3.4 worms/fish). Similarly, prevalence of this parasite in Wye River eels increased from 29% in spring 1997 to 37% in fall 1998, and 53% in fall 1999 (Table II). Most likely, the longer this parasite is present in Chesapeake eel populations, the faster it will spread within the estuary. A rapid increase in *A. crassus* distribution has been noted in European eel populations in Denmark by Køie (1991); Kennedy and Fitch (1990) observed that prevalence of *A. crassus* reached 100% within 1 yr of being introduced to a river in eastern England. Höglund and Andersson (1993) saw an increase in prevalence of *A. crassus* within the first 3 yr of its existence in a brackish water bay in the Baltic Sea off the coast of Sweden. Rapid population increase is attributed, in part, to a low degree of specificity for intermediate and paratenic hosts (Höglund and Thomas, 1992; Moravec and Konecny, 1994; Moravec, 1996; Moravec and Škoríková 1998) and the ability to colonize across a wide range of salinity and temperature regimes (Reimer et al., 1994; Knopf et al., 1998; Kirk, Kennedy, and Lewis, 2000; Kirk, Lewis, and Kennedy, 2000).

In our study, greater numbers of eels than predicted were either infected with both adult and juvenile nematodes or were uninfected; fewer eels than predicted were infected with adults only or juveniles only. Ashworth and Kennedy (1999) found that the number of juvenile nematodes per eel increased when adult subpopulation size was large, and this was attributed specifically to inhibition of juvenile migrations into the lumen of the swimbladder. This increased residence time of juveniles in the swimbladder wall when adult nematodes are present in the lumen could contribute to the increased number of eels infected with both adults and juvenile worms. Greater susceptibility to infection among already infected eels might also play a role in explaining this nonrandom distribution pattern of adult and juvenile *A. crassus*.

The relative contribution of *A. crassus* infections to the natural mortality of American eels is not known. Kirk, Lewis, and Kennedy (2000) reported numerous pathological changes to eel swimbladders caused by *A. crassus*. These authors further proposed that because migrating silver eels undergo daily vertical migrations, infections might impair the ability of eels to migrate to the Sargasso Sea to spawn. Further study is needed to determine the potential effects of *A. crassus* on all life stages of the American eel and throughout its range in North America.

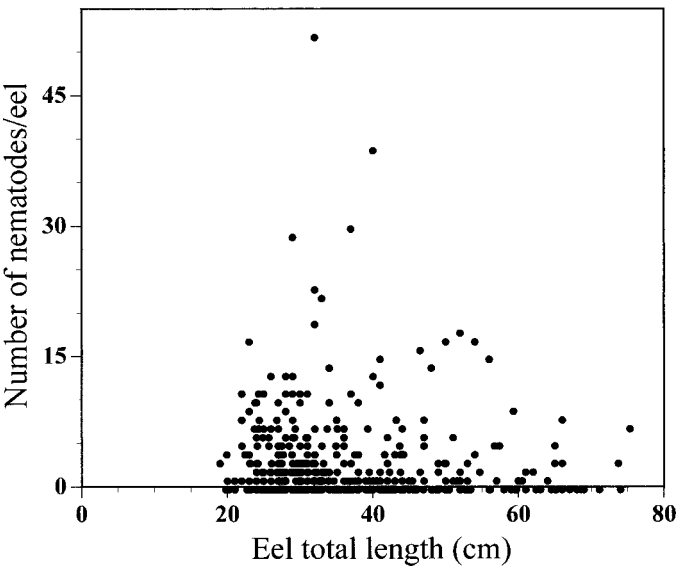

FIGURE 2. Scatterplot of eel length (cm) vs. intensity of infection with *Anguillicola crassus*.

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