Am. Midl. Nat. 129:301–308

Feeding Selectivity of the American Eel Anguilla rostrata (LeSueur) in the Upper Delaware River

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ABSTRACT.—The population of American eels *Anguilla rostrata* (LeSueur) residing in the Upper Delaware River was sampled monthly from May through August 1986. Gastric examination of 325 eels captured by electrofishing revealed that 154 (47%) were empty and 171 (53%) contained food items. The specimens examined contained 2992 organisms of 59 taxa (four fish and 55 macroinvertebrate) and three non-organism categories.

Macroinvertebrates, predominantly of the Class Insecta, were eaten by 169 eels (99% of feeding eels). The orders Ephemeroptera and Plecoptera occurred most often in eel stomachs (69%). The stonefly *Acroneuria* was the single most numerically dominant taxon observed in the diet, occurring in 67% of eel stomachs that contained food. Fishes were consumed by 12 eels (7%).

The clustering near zero of electivity values for the overall study suggests that eels feed opportunistically on many macroinvertebrate taxa. The values also indicate that five food taxa were significantly ($P < 0.05$) selected as prey by American eels: Baetidae, *Drunella,* Perlidae, *Hydropsyche* and Polycentropodidae. The orders Ephemeroptera, Plecoptera and Trichoptera accounted for 92.7% of the organisms consumed, although they comprised 48.1% of the available organisms. Ten food taxa were significantly ($P < 0.05$) avoided as prey by eels: Planaridae, Oligochaeta, Pelecypoda, Gastropoda, Gammaridae, *Cheumatopsyche, Lepidostoma,* Elmidae larvae, Dipteran pupae and Chironomidae. The insect orders Diptera and Coleoptera and the phylum Gastropoda accounted for 4.8% of the organisms consumed, although they comprised 32% of the available organisms.

INTRODUCTION

Little is known about the feeding behavior of the American eel *Anguilla rostrata* (LeSueur) (Helfman, 1986), despite the fact that anguillid eels are one of the most-studied families of fish in the world and the American eel is widely distributed throughout the Atlantic and Gulf slopes of North America (Lee, 1980). The early hypothesis that the American eel was a scavenger (Jordan and Evermann, 1923; Perlmutter, 1974; Moriarty, 1978) was questioned when Tesch (1977) observed that eels did not eat decayed meat. The majority of diet, food habits and feeding behavior studies of the American eels have shown that the diet is comprised primarily of invertebrates and small fishes. The purposes of this study are to document the taxa consumed by the American eel in the Upper Delaware River and to compare the relative abundances of these taxa in the eel diet to that in the environment.

MATERIALS AND METHODS

Description of study area.—Sampling was conducted in the Delaware River 11 km downstream of Pond Eddy in Sullivan County, New York. All collections were made within a 200 m reach along the New York shore of the river immediately downstream of Mongaup Island. The study area is located within the Upper Delaware National River, and this section of water is classified as a wild and scenic river. In the study area, the river is approximately 150 m wide and reaches a depth of 2.2 m. Substrate is composed primarily of boulders (rocks greater than 25 cm in diam) and cobble (6–25 cm) with gravel, sand and silt filling interstitial spaces and settling in slower flowing areas along the shoreline.

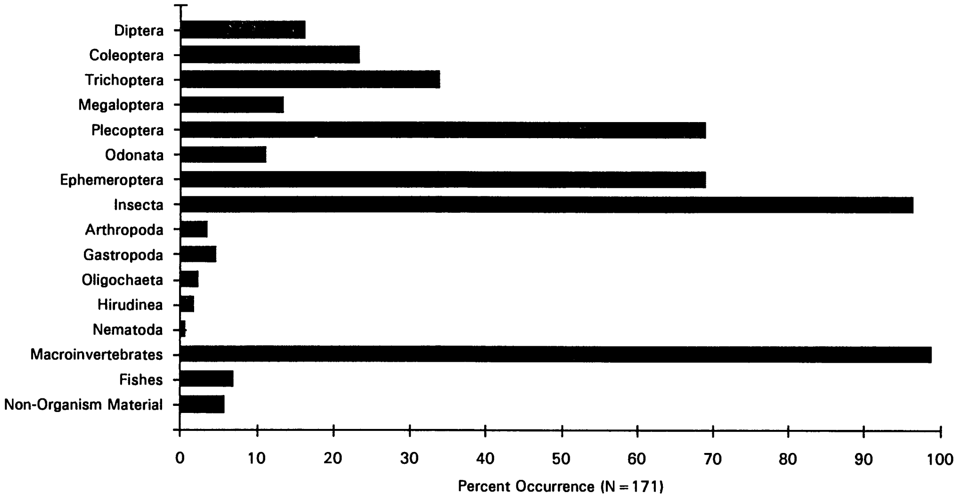

FIG. 1.—Percent occurrence of food items in stomachs of American eels collected in the upper Delaware River during May–August 1986

Sample collection.—Four fish community and one benthic macroinvertebrate samples were taken within a 24-h period each month between May and August 1986. Each sampling effort was completed within 24 h and consisted of four separate sampling periods—noon, 1 h before sunset, 1 h after sunset and 1 h after sunrise.

Fishes were collected using current from a 110-volt (AC) Honda portable electric generator housed in a small boat and pulled behind the collectors. Fish samples provided a minimum of 15 eels, which were retained per sample period and preserved in 20% formalin to ensure complete preservation of the stomach contents. The coelom was slit on larger specimens (>35 cm) to inhibit post-capture digestion. Macroinvertebrates were collected by vigorously disturbing the river bottom immediately upstream of a D-frame kick net. Nine 20-sec kick samples were collected and preserved in 10% formalin.

Laboratory handling of samples.—Macroinvertebrate samples were sorted, identified to the lowest practicable taxon (usually genus) using keys provided in Merritt and Cummins (1984) and enumerated. Fishes were sorted, identified to species, enumerated, transferred to 50% isopropanol and placed in permanent storage in The Pennsylvania State University Fish Museum.

Eels were measured to the nearest half centimeter, weighed and eviscerated. Eel stomachs, consisting of the blind sac of the pylorus, were removed from the eels and weighed. The stomachs were opened and the contents gently washed into dishes for identification. Food items removed from eel stomachs were identified in a manner consistent with the macroinvertebrate samples and transferred to 50% isopropanol.

Sample analysis.—The number of eels consuming specific food items was tabulated by month. Percent occurrence values for the overall study were calculated for individual food items by comparing the number of eels that contained a particular food taxon with the number of eels containing food items (Hyslop, 1980).

Strauss' (1979) Linear Index (L) was used to determine the relationship between the relative abundance of each food item in the diet (r) and the relative abundance of prey items in the environment (p). Index values were calculated through the use of a public domain environmental statistics package called Ecomeasures (Kotila, 1987). Strauss' L was selected due to its linear and symmetrical deviation for all r not equal to p (Lechowicz, 1982); therefore, a change in r and p values has the same effect at all values of r and p.

Index values were calculated predominantly at the family level or above due to limitations imposed by Kotila's (1987) electivity indices calculating program and the observation by Bowen (1983) that studies performed in the past 10 yr providing the greatest insight into trophic ecology of fish used feeding comparisons at higher taxonomic levels (family or order).

The mean, standard deviation and 95% confidence intervals were calculated for each monthly set of electivity data and for the overall study results.

RESULTS AND DISCUSSION

Stomach contents.—Gastric examination of 325 eels revealed that 171 (52.6%) had contents in their stomachs. The stomachs contained 2992 organisms representing 56 taxa. The stomachs of 154 eels were empty. The eels consumed four fish taxa, 52 macroinvertebrate taxa and three nonorganism categories. This was consistent with other stream studies of American (Godfrey, 1957; Ogden, 1970; Facey and LaBar, 1981) and European eels (Frost, 1946; Thomas, 1962; Sinha and Jones, 1967).

The number of organisms observed in stomachs ranged from 1–145 with an average of 17.6 organisms. The number of taxa observed in stomachs ranged from 1–12 with an average of 4.4. Four stomachs contained detritus or vegetation, four contained bits of bone and flesh, and two contained sand and gravel.

Fish consumption.—Fishes were observed in 12 (7.0%) of the feeding eels examined (Fig. 1). Fish in five of the eels stomachs were digested beyond visual identification. Identifiable prey fishes included three sea lamprey ammocetes (*Petromyzon marinus*), three margined madtoms (*Noturus insignis*) and one minnow (*Notropis* sp.). Two of the prey fishes were observed in May, three in June, one in July, and six in August. None of the 12 piscivorous American eels consumed more than a single fish, although 10 had also fed on macroinvertebrates. Facey and LaBar (1981) observed fish in 26% of the feeding American eels examined in their study. This percentage was considerably higher than levels observed in the present and previous studies of American and European eels [Frost, 1946 (<1%); Godfrey, 1957 (10%); Sinha and Jones, 1967 (5%); and Ogden, 1970 (14%)]. Facey and LaBar (1981) attributed the high percentage of fish prey to the large mean length of eels examined in their study. Other studies (Frost, 1946; Sinha and Jones, 1967; Ogden, 1970) observed that large eels (>45 cm) had a tendency to consume more fishes than small eels (<40 cm). The mean length of piscivorous eels observed in our study (37 cm) was greater than the mean length of eels feeding on macroinvertebrates (33 cm). The Mann Whitney test, however, revealed no statistically significant difference ($P < .05$) in length between these two groups.

Piscivorous eels in the present study contained a lower mean number of food items (5.1 compared to a 17.6 study mean), and a lower mean number of food taxa (3.2 compared to a 4.4 study mean) than other eels. Statistical comparison between American eels that consumed fish and those that consumed macroinvertebrates using a Mann Whitney test revealed a statistically significant ($P < .05$) difference in the number of food items but not in the number of food taxa. These data suggest that eels may be satiated after opportunistically obtaining a large prey item (fish), or that they may have consumed fish at the end of an unsuccessful feeding period. Ryan (1984) observed that activity in short-finned eels, *Anguilla australis schmidtii* (as determined by catch rates) continued beyond sunrise in spring and summer. He hypothesized that this continued activity might have been due to unsuccessful nocturnal feeding. Although seven of the 12 piscivorous eels observed were collected

TABLE 1.—Strauss's linear L (×1000) comparing invertebrates observed in kick samples and in the stomachs of 171 eels collected in the upper Delaware River in 1986. Boldface indicates prey significantly selected or avoided at $P < 0.05$

Taxon	May	June	July	August	Overall
Turbellaria					
Planaridae	−11	**−81**	**−48**	−25	**−30**
Hirudinae	2		2	2	2
Oligochaeta	1	11	−11	**−100**	**−17**
Pelecypoda	−13	**−49**	**−82**	**−45**	**−36**
Gastropoda	**−53**	**−35**	**−106**	**−272**	**−95**
Crustacea					
Cambaridae	−10	−3	2	5	−4
Gammaridae		−22	**−77**	−9	**−18**
Insecta					
Ephemeroptra					
Baetidae sp.	**70**	**116**	**265**	**504**	**206**
Caenidae					
Caenis	−6	**−54**	−14	−6	−15
Ephemerellidae	16	23	24	6	−5
Drunella	**69**	23			**31**
Ephemeriidae	−1	8	−1		2
Heptageniidae	**−28**	**59**	**28**	12	6
Leptophlebiidae	1				0
Oligoneuridae					
Isonychia	11	−3	5	21	0
Odonata					
Zygoptera			2		0
Coenagrionidae	−15	−5		−2	−9
Anisoptera	1	2	2		1
Corduliidae	1	2	2	2	1
Gomphidae	3	2	−3	2	2
Macromiidae					
Macromia	−1			0	0
Plecoptera					
Perlidae	**263**	**149**	7	25	**144**
Perlodidae					
Isoperla	12				5
Taeniopterygidae	−1				0
Hemiptera					
Microvelidae					
Metrobates		−2			
Megaloptera					
Corydalidae					
Corydalus	19	0	0	7	9
Sialidae					
Sialis		−15	−5	−3	−4
Trichoptera					
Adult spp.	2		2		1
Pupae spp.	−3		−9	−5	−4
Brachycentridae					
Brachycentrus		−3		−2	−1

TABLE 1.—Continued

Taxon	May	June	July	August	Overall
Helicopsychidae					
Helicopsyche	−1		−5	−8	−2
Hydropsychidae					
Cheumatopsyche	−15	**−43**	**−29**	**−81**	**−32**
Hydropsyche	5	**186**	**173**	−6	**77**
Macronema				−14	−2
Hydroptilidae	−2		−11	−2	−3
Lepidostomatidae	2			9	2
Lepidostoma	**−30**	−20	**−34**	−11	**−26**
Leptoceridae	**−27**	−15	**58**	−6	−4
Limnephilidae					
Hydatophylax		5	0		1
Philopotamidae					
Chimarra			−15	−8	−4
Phrygaenidae		2	2	2	1
Polycentropodidae	4	−8	**42**	**69**	**23**
Psychomyiidae		11	−6	−3	1
Lepidoptera					
Pyralidae				−2	0
Coleoptera					
Elmidae					
Adult spp.	−9	−2	−3	−25	−11
Larvae spp.	**−51**	**−50**	**−32**	**−58**	**−49**
Gyrinidae					
Gyrinus	−4				−2
Halipidae					
Berosus	−2				−1
Psephenidae					
Psephenus	0	13	35	13	13
Diptera					
Pupae spp.	**−45**	−10	9	18	**−18**
Ceratopogonidae		−2	−2		−1
Chironomidae	**−158**	**−176**	**−156**	−7	**−136**
Empididae	−1		0		0
Simuliidae			−3	7	1
Tipulidae	1	−3	−5	−5	−2
Number of values	42	37	42	41	54
Mean	−0.10	0.03	0.07	−0.02	−0.04
Standard deviation	53.10	59.03	62.95	94.70	44.77
Upper 95% conf. int.	16.45	19.71	19.69	29.90	12.19
Lower 95% conf. int.	−16.64	−19.66	−19.55	−29.90	−12.26

after sunrise, five of these seven prey fishes were unidentifiable due to advanced decomposition. This implies that these fishes had been in the stomach for several hours.

Macroinvertebrate consumption.—Macroinvertebrates were observed in 98.8% (169 eels) of the feeding eels examined (Fig. 1). The Class Insecta constituted 47 of the 52 macroinvertebrate taxa observed. Mayflies (Ephemeroptera) and stoneflies (Plecoptera) were observed in 118 of 171 feeding American eels (69%). Percent occurrences of other insect

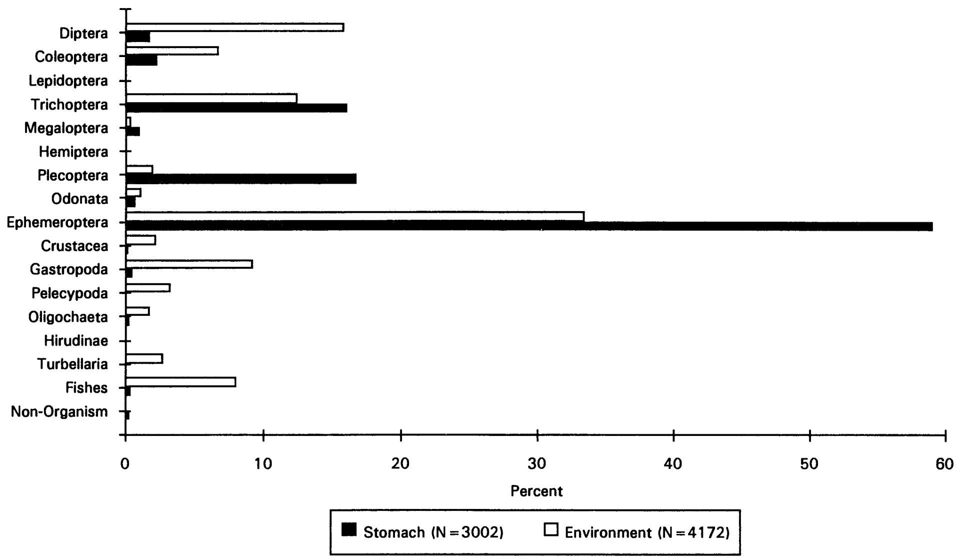

FIG. 2.—Relative abundance (percent) of items observed in samples from the prey base and American eel stomachs during May–August 1986

orders consumed by eels were caddisflies (Trichoptera) 33.9%, beetles (Coleoptera) 23.4%, flies (Diptera) 16.4%, fishflies and hellgrammites (Megaloptera) 12.8%, and dragonflies and damselflies (Odonata) 11.1% (Fig. 1). This is consistent with the results of earlier studies of American eels (Godfrey, 1957; Sinha and Jones, 1967; Ogden, 1970; Wenner and Musick, 1975; McCord, 1977; Facey and LaBar, 1981; Helfman, 1986; Helfman and Clark, 1986).

Monthly electivity of feeding.—Electivity values were calculated for 54 taxa of invertebrates (Table 1). Fishes and non-organism categories were excluded from electivity calculations due to the low percent occurrence of these items in the eel diet. Electivity values ($\times 1000$) ranged from -0.272 to 0.504, although the majority of the values fell between -0.030 and 0.030.

Mean electivity values were near zero for all sets of electivity values, monthly and overall (Table 1). The clustering near zero of electivity values of the overall study suggests that eels feed opportunistically on many macroinvertebrate taxa. The values also indicate that five of 54 food items evaluated were significantly ($P < 0.05$) selected as prey by American eels: Baetidae, *Drunella,* Perlidae, *Hydropsyche* and Polycentropodidae (Table 1). The orders Ephemeroptera, Plecoptera and Trichoptera accounted for 92.7% of the organisms consumed, although they comprised 48.1% of the available organisms (Fig. 2). Ten taxa were significantly ($P < 0.05$) avoided as prey by eels: Planaridae, Oligochaeta, Pelecypoda, Gastropoda, Gammaridae, *Cheumatopsyche, Lepidostoma,* Elmidae larvae, Dipteran pupae and Chironomidae (Table 1). The insect orders Diptera and Coleoptera and the phylum Gastropoda accounted for 4.8% of the organisms consumed, although they comprised 32% of the available organisms (Fig. 2).

Heptageniidae and Leptoceridae were the only food items both significantly avoided and selected by feeding eels during different months (Table 1). Electivity values for Leptoceridae indicated significant avoidance in May, avoidance in June and August, and significant selection in July. The shift in Leptoceridae electivity was due to a large increase in the numbers observed in eel stomachs, not a change in abundance in the environment. The reason eels suddenly began consuming Leptoceridae is not known, but it may be due to changes in availability of these caddisflies during emergence.

The shift from significant avoidance (May) to selection (June) for Heptageniidae may be due to the abundance of *Acroneuria* during the May sampling event. These large stoneflies would have been readily available to eels as food items during their migration from the bottom of the river to the shoreline to begin their metamorphosis from aquatic nymphs into adults. The availability of these large stoneflies in high numbers is probably responsible for the selection of fewer Heptageniidae than were available in the environment (Table 1). *Acroneuria* was observed in the stomachs of 52 of 61 feeding eels collected in May, while Heptageniidae were observed in 23 stomachs. The relatively low number of *Acroneuria* observed in the environment in May could reflect the loss of a large percentage of the population emerging during the night prior to collection of the benthic macroinvertebrate sample.

Unexpectedly, June and July electivity values imply that eels significantly selected the genus *Hydropsyche* while significantly avoiding the genus *Cheumatopsyche* (Table 1). These two genera, both members of the caddisfly family Hydropsychidae, are very similar morphologically and are often difficult to differentiate in the laboratory under a microscope.

The negative association implying avoidance of Chironomidae observed in this study is consistent with results of earlier investigations (Frost, 1946; Burnet, 1952, in Ryan, 1984; Thomas, 1962; Sinha and Jones, 1967; Moriarty, 1978; Ogden, 1970; De Nie, 1987). When an array of food items provided eels with the option to choose between substrate-dwelling mayflies and caddisflies or Chironomidae, the chironomids were numerically unimportant in the diet.

General observations.—The macroinvertebrates observed in stomachs showed little disfigurement due to mastication or digestion. The lack of disfigurement greatly assisted the identification of stomach contents to the genus level. The lack of disfigurement observed in this study implies that holding time within the blind sac of the pylorus was minimal and that information obtained from the eel stomachs probably reflected what the eel had been eating a short time prior to capture. Ryan (1984) observed that short-finned eels had a 6-h gastric evacuation time for macroinvertebrates.

The monthly benthic macroinvertebrate samples contained 3832 specimens of 68 taxa and showed little variation in community structure. The monthly fish prey base samples contained 340 specimens representing 17 species. Little variation was observed in species richness among monthly samples of the fish community.

The data indicated that eels fed opportunistically on many macroinvertebrate taxa, although five taxa were preferred: Baetidae, *Drunella,* Perlidae, *Hydropsyche* and Polycentropodidae. The orders Ephemeroptera, Plecoptera and Trichoptera comprised 92.7% of the organisms consumed, although they constituted only 48.1% of the available organisms in the environment. Conversely, the orders Diptera and Coleoptera and the phylum Gastropoda accounted for 4.8% of the organisms consumed, although they represented 32% of total number of organisms in the environment.

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SUBMITTED 26 FEBRUARY 1992 ACCEPTED 3 AUGUST 1992