Environ Biol Fish (2024) 107:513–522
https://doi.org/10.1007/s10641-024-01544-z

Check for updates

# An experimental study of benthic habitat selection in yellow-phase American eels (*Anguilla rostrata*)

**Melissa A. Braham · Stuart A. Welsh · Dustin M. Smith**

Received: 12 December 2023 / Accepted: 21 March 2024 / Published online: 14 May 2024


**Abstract** In a laboratory experiment, we quantified microhabitat use of small yellow-phase American eels (*Anguilla rostrata*, $n = 130$, 224–338 mm TL) conditional on five benthic substrate types common to rivers within their geographic range. During nine, 4-day trials replicated with three aquaria, American eels were given a choice to burrow into five equally available benthic substrates: cobble (90–256 mm), gravel (4–16 mm), sand (0.125–1 mm), silt/clay ($< 0.0625$ mm), and leaf pack. Five American eels were used per aquarium for each trial, and individuals were used one time only. All eels were injected with PIT tags prior to the study, which allowed for determination of lengths and otolith-based ages of each individual following each trial. Leaf pack was selected with a significantly higher probability than other substrates (63 of 130 individuals). However, other substrates were also used (cobble, 21 of 130; silt/clay, 18 of 130; gravel, 16 of 130; and sand, 12 of 130). Length and age covariates were not associated with substrate selection. Selection of leaf pack habitat supports the importance of forested riparian zones and terrestrial organic material to yellow-phase American eels in riverine systems.

**Keywords** Microhabitat preference · Substrate selection · Leaf pack · Riverine riparian zones

M. A. Braham
Conservation Science Global, Cape May, NJ 08204, USA

S. A. Welsh (✉)
U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, WV 26506, USA
e-mail: swelsh@wvu.edu

D. M. Smith
West Virginia Division of Natural Resources, Farmington, WV 26571, USA

## Introduction

The complex life history of the facultatively catadromous American eel (*Anguilla rostrata*) includes occupancy of freshwater habitats (Tesch 1977; Fahay 1978). Studies have examined the life history of yellow-phase eels in freshwater, including upstream migration and establishment of home ranges (Bozeman et al. 1985; Oliveira 1997; Welsh et al. 2016). Yellow-phase American eels have strong nocturnal tendencies, commonly foraging at night, and presumably seeking refuge during daytime (Meffe and Sheldon 1988; Goodwin and Angermeier 2003; Hedger et al. 2010; Tomie et al. 2013). Additionally, yellow-phase eels are known to associate with benthic habitat, often spending most of their time burrowed in benthic substrate (Tomie et al. 2017).

Habitat studies on American eels have found a wide range of habitat use at broad sampling scales across seasons. During fall, Meffe and Sheldon (1988) found large American eels in muddy leafy substrates and small eels in muddy, sandy substrates. Goodwin and Angermeier (2003) sampled from late spring through fall and reported high catch rates of large American eels in leaf pack and other organic materials. Similarly, Johnson and Nack (2013) reported autumnal use of leaf pack habitat in a tributary of the Hudson River. During summer, Ford and Mercer (1986) observed large and small American eels in soft mud bottomed substrates but also observed large eels in sandy substrates. Modeling studies of Smogor et al. (1995) and Wiley et al. (2004), based on data collected from summer through early fall, did not find significant habitat associations of American eels in relation to substrate.

Microhabitat studies, particularly laboratory experiments such as that of Tomie et al. (2017), have been rarely conducted on substrate selections of yellow-phase American eels. Additional studies would be beneficial for understanding habitat use by yellow-phase eels, particularly given that population decline is a concern for this species, and that the loss and alteration of freshwater habitats may contribute to population decline (Haro et al. 2000; Casselman 2003; Drouineau et al. 2018). Studies on benthic habitat use have been encouraged by authors of review papers on population decline of the American eel (Castonguay et al. 1994; ASMFC 2000; Haro et al. 2000), the findings of which may benefit our understanding of American eel ecology as well as conservation and management planning for the species (ASMFC 2023). The objective of this study was to determine yellow-phase American eel microhabitat selection for or against five benthic substrate types. We also examined the relationship of length and age with microhabitat selection. Although results are conditionally-based on five benthic habitat types, information from this laboratory study may be applicable to our understanding of yellow-phase American eel selection of riverine microhabitats, given that the experimental benthic substrates are common to many Atlantic Coast drainages.

## Methods

### Field sampling

A total of 150 yellow-phase American eels were collected during summer (July) from an eel ladder at the Millville hydroelectric dam, Shenandoah River, West Virginia. All individuals were transported to the laboratory in coolers with aerated stream water. The Millville hydroelectric dam is located approximately 9 km upstream from the confluence of the Potomac and Shenandoah rivers, 100 km upstream of the Potomac River at head of tide, and 285 km upstream from the mouth of the Potomac River estuary.

### Laboratory setup

Within the laboratory, the 150 American eels were subdivided into four holding tanks and acclimated to the laboratory setting prior to the substrate experiment. Each holding tank system encompassed two 378.5 L plastic tanks (132.1 × 78.7 × 63.5 cm) and one 378.5 L plastic sump (132.1 × 78.7 × 63.5 cm). Approximately two weeks before the experiment, eels were anesthetized with Tricaine methanesulfonate (MS-222) and tagged anterodorsolaterally with passive integrated transponder tags (PIT) and measured to the nearest mm TL (Zimmerman and Welsh 2008). The PIT tags provided identification for each individual and allowed for analysis of relations among length, age, and microhabitat selection.

The experimental system encompassed three glass aquaria (473.2 L; 184.2 × 47.0 × 59.4 cm) and one 378.5 L plastic sump (132.1 × 78.7 × 63.5 cm). Both the holding and the experimental systems used recirculation systems where water was gravity fed from aquaria to the sump and pumped, using a 1/8 horsepower sequence pump, back into the aquaria. The water level in each aquarium was approximately 33 cm (23 cm below the top), which prevented eels from escaping. Each aquarium had five equally available substrates in separate removable, 39.4 cm long by 29.2 cm wide by 21.1 cm deep, plastic bins. The bottom of each aquarium was covered with foam (New England Foam, Hartford, Connecticut; 21.1 cm deep) with five rectangular areas cut out to match the outside dimensions of the substrate bins. The 21.1 cm deep bins fit into the 21.1 cm deep cut outs, where the top of the foam was flush with the top of the bins. Thus, an eel had the option to occupy any of the five substrate bins or rest on top of the adjacent foam.

Five substrates were tested during this experiment: cobble (90–256 mm, measured across the longitudinal axis), gravel (4–16 mm), sand (0.125–1 mm), silt/clay (< 0.0625 mm), and leaf pack. These five substrate types, obtained from the Potomac River drainage, were chosen based on their commonality to American eel habitat in many North American rivers, and because of their use in other American eel habitat studies (Tesch 1977; Ford and Mercer 1986; Meffe and Sheldon 1988; Goodwin and Angermeier 2003). The cobble, gravel, sand, and silt/clay classifications were based on a modified Wentworth grain scale (Wentworth 1922). The gravel, sand, and silt/clay substrates were dried in an oven and separated using U.S. and metric standard testing sieves and a vibratory sieve shaker (Retsch GmbH., Haan, Germany). The leaf pack substrate was rinsed with filtered water and dried to remove mud and potential invertebrates. The leaf pack consisted mainly of maple (*Acer* spp.), sycamore (*Platanus occidentalis*), tulip poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), American beech (*Fagus grandifolia*) and birch (*Betula* spp.) leaves. We were concerned that one or more leaves from the pack could be dislodged by the burrowing motion of an eel, causing contamination of an adjacent substrate bin. To address this concern, we covered the leaf pack bin with a loose mesh of monofilament fishing line (0.11 mm diameter) which allowed entrance and exit of eels within the leaf pack.

## Experimental design

The substrate use experiment (July–August) consisted of nine trials during which five randomly chosen eels from holding tanks were released into each of the three aquaria. On the fourth day of the trial, the substrate bins were fitted with plastic lids during daylight hours, removed from aquaria, and inspected for the presence of eels. After recording counts of eel presence and PIT tag numbers, the post-trial eels were prepared for age determination (see methods below), and new individuals were released into the aquaria until all subsequent trials were completed.

Eels are known to have a strong sense of smell (Tesch 1977; Facey and Van Den Avyle 1987); therefore, precautions were taken to reduce an influence of eel scents in substrates among trials. Two sets of substrates with plastic bins were used during the experiment. In between the trials, substrates from the prior trial were spread onto a surface to dry while the second set of substrate bins were randomly placed back in the aquarium for the next trial. During this time we revaluated the amount of substrate in each bin and added more to maintain equal substrate amounts throughout the study period. Substrates were kept at an approximate level of 7.6 cm from the top of the plastic bins, which reduced substrate losses during eel burrowing.

## Water quality

In holding and experimental tanks, water quality was monitored daily for conductivity, total ammonia nitrogen, temperature, dissolved oxygen, unionized ammonia, nitrite, hardness, alkalinity, and visual inspections of turbidity/algae. To maintain water quality, we used a charcoal filter in the inflow to the sump, ammonia was controlled by ammonia towers (bio balls) in the sump along with sponge-filter aeration, and an ultraviolet light was used to sterilize water. Aquarium water temperatures fluctuated between 14–18°C. The photoperiod was 12 h of light and 12 h of dark throughout the experiment. Eels were fed daily with frozen enriched bloodworms (Hikari, Hayward, California; San Francisco Bay Brand Inc, Newark, California) and brine shrimp (San Francisco Bay Brand Inc, Newark, California). Food was evenly distributed in the aquaria in an effort to not influence substrate bin selection.

## Age determination

After aquarium experiments, PIT-tagged eels were euthanized for otolith removal. Ages of American eels were determined by counting annual rings of the sagittal otolith. Eel otoliths are known to contain complete and incomplete false annuli (Liew 1974; Oliveira 1996; Morrison and Secor 2003), and bias from false annuli was reduced by following aging techniques of Oliveira (1996). Sagittal otoliths were exposed by a lateral cut through the top of the head cavity. The pair of otoliths was then removed, cleaned of extraneous tissue, and stored in a labeled coin envelope for subsequent processing and analysis. One of each pair of otoliths was embedded in epoxy resin for 48 h or until hardened. The otoliths were transversely sectioned to an approximate 0.18 mm thickness using an Isomet low speed saw (Buehler Inc. Lake Bluff, Illinois). Sections were then etched for three to five minutes with 5% ethylenediaminetetraacetic acid (EDTA) with a pH of 6 and stained for two to three minutes with 0.01% toluidine blue

(Oliveira 1996). The stain treatment enhanced the accuracy of age estimation, in part because transmitted light through blue opaque (summer) zones aided in the differentiating of false annuli. Sections were then read, by two independent readers, under transmitted light with a stereoscope using 100× magnification. The two readers assessed the readability of each otolith using the following grades; (0 = unreadable, 1 = low readability, 2 = mid readability, and 3 = high readability). This was done to aid in the finding of a consensus age. If a consensus age was not reached, due to poor readability, the otolith was rejected and the second otolith, if present, was prepared as stated above. For this study ages were represented by the inland years; the hyaline center (i.e., sea years) was not included for age determination.

### Statistical analysis

Initially we conducted a Chi-square test of the null hypothesis that American eels were randomly selecting substrate types in proportion to availability (Manly et al. 2002). This test determined whether there was a significant difference between the expected use of substrate types and the observed frequency of use (Neu et al. 1974; Byers et al. 1984; Manly et al. 2002). In the habitat use experiment, substrate types were available in equal proportions; hence, "substrate selection" was equivalent to "substrate preference" as defined by Johnson (1980). Following the initial Chi-square analysis, we fit multinomial logistic regression models to the data (Hosmer and Lemeshow 2000; Agresti 2002; Manly et al. 2002), which examined the influence of explanatory variables on eel substrate selection. Models specified substrate selection as functions of trial, aquarium, TL, and age. However, use of explanatory variables resulted in a sparse dataset, owing to an absence of continuous age and length data within some aquarium and trial categories. Due to the sparseness of the data, we used two separate multinomial logistic regression models for the two data types (categorical and continuous). The first set of models specified the substrate selection as functions of trial and aquarium while the second set of models specified the substrate selection as functions of TL and age. The leaf pack substrate was used as the baseline category for both sets of models. Each of the equations modeled the logit, which was the log of the ratio of the probability of selection for a particular substrate and the probability of selection for the leaf pack substrate (baseline category). To evaluate models, we compared the difference in deviance (2*max log-likelihood of the fitted model /max log-likelihood of the saturated model) between the saturated model and the fitted model. Model fit was assessed using deviance, which follows a chi-square distribution (Hosmer and Lemeshow 2000). Additionally, descriptive statistics were plotted for the proportions of the five equally available substrate types used by yellow-phase American eels. Variation associated with each proportion was calculated as 95% profile likelihood confidence intervals.

To determine if American eels selected for or against a certain substrate type, odds ratios were derived from the multinomial logistic regression model. Odds ratios are measures of association which range from zero to infinity, and require the designation of one category as a reference (Hosmer and Lemeshow 2000). An odds ratio was estimated for each substrate type, and leaf pack was used as the "baseline category." An odds ratio greater than one supports selection for a substrate type instead of leaf pack (baseline category), where odds ratios less than one indicate selection against a substrate type instead of leaf pack. An odds ratio of one implies that the selected substrate is equally likely in both categories (Hosmer and Lemeshow 2000). To test the odds ratios, 95 percent confidence intervals were calculated. The odds ratios were considered significant if the intervals did not contain a value of one. Computations were conducted using Microsoft Excel (2007) and the R software (R Development Core Team 2009).

## Results

A total of 150 yellow-phase American eels were collected at the Millville hydroelectric site. We used 135 individuals for the 9 trials. At the completion of the 9 trials, 130 out of 135 individuals used a substrate type while the remaining five individuals did not burrow or reside within any of the substrates provided. These five individuals were removed from the data analysis. All 130 eels burrowed into the substrate, but we did not determine depth of the eels within the substrate bins. The American eels used in this study had a TL range of 224–338 mm (mean 273 mm, SE 2.34; Fig. 1a). The American eel consensus ages ranged between 3–11 years (mean 6 years, SE 0.157; Fig. 1b). Otoliths from 13 of the 130 eels were deemed unreadable by both readers. The 13 unreadable otoliths along with their associated lengths were also not used in the multinomial logistical regression analysis of substrate selection.

Comparing the multinomial logistic regression deviances of the different models suggested the trial and aquarium did not have a significant effect on eel selection of a particular substrate type (Table 1). All models compared to the saturated model (maximum number of parameters) did not show a significant *p*-value ($\alpha = 0.05$) and allowed the data to be collapsed across aquaria and trial for further analysis.

Yellow-phase American eels did not use substrate at the expected ratio of 1/5 ($X^2 = 67.462$; df = 4; $p < 0.005$). Of the five substrate types provided, leaf pack was used by 63 of 130 (48.5%), cobble was used by 21 of 130 (16.2%), silt/clay was used by 18 of 130 (13.8%), gravel was used by 16 of 130 (12.3%),

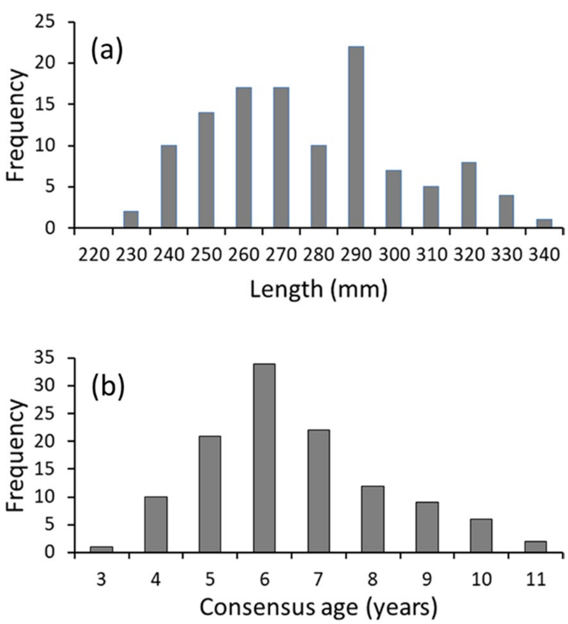


**Fig. 1** Total length (**a**) and age (**b**) frequencies of 117 yellow-phase American eels collected at the Millville Dam eel ladder and used during the substrate selection laboratory study. Lengths ranged from 224 to 338 mm (mean = 273 mm, standard error = 2.34). Length categories are 10 mm intervals (e.g. the 230 length category represents eel lengths from 221 to 230 mm). Consensus ages ranged from 3 to 11 years (mean = 6 years, standard error = 0.157)

**Table 1** Deviance statistics from a multinomial logistic regression analysis assessing the influence of aquarium and trial categories on substrate selection by American eels

| | Df | Deviance | LR ($G^2$) | *P*-value |
|---|---|---|---|---|
| Saturated | --- | --- | --- | --- |
| Null | 104 | 363.24 | 105.21 | 0.448 |
| Aquarium | 96 | 358.67 | 100.64 | 0.353 |
| Trial | 72 | 318.02 | 59.99 | 0.843 |
| Aquarium + Trial | 64 | 313.08 | 55.05 | 0.780 |

and sand was least used by 12 of 130 (9.2%; Table 2; Fig. 2). Using leaf pack as the baseline category, the odds ratio of an eel choosing any of the other substrates was less than one, indicating that selection of other substrates was not as likely as that of choosing leaf pack. The calculated 95% confidence intervals did not contain a value of one, therefore the odds ratios were significant ($\alpha = 0.05$). The other substrate types (cobble, gravel, sand, and slit/clay) odds ratios were then compared to one another and we found no significant ($\alpha = 0.05$) ratios among them.

After collapsing the selection data across aquaria and trial, we examined substrate use as a function of length and age. Box plots did not visually depict differences in American eel lengths or ages among substrate categories (Fig. 3). To test this, we modeled the length and age substrate selection data as continuous in the multinomial logistic regression model. The analysis of deviance, from the multinomial logistic regression, indicated that discarding any one of the TL and age covariates from the saturated model had no influence on the American eel substrate selection (Table 3).

## Discussion

In this laboratory study, yellow-phase American eels selected leaf pack over other available benthic substrates. Although leaf pack was the preferred substrate, American eels also used cobble, gravel, sand, and silt/clay substrates. American eels have been categorized as habitat generalists (Helfman et al. 1987), which has been supported by field studies reporting a wide range of substrates, including mud, cobble, gravel, sand, and leaf pack (Tesch 1977; Ford and Mercer 1986; Meffe and Sheldon 1988; Goodwin and

**Table 2** Total number and percentage of yellow-phase American eel selecting each substrate

| Substrate type | # of eels | % of eels | odds ratio | SE | 95% CI | |
|---|---|---|---|---|---|---|
| Leaf pack | 63 | 48.5 | 1.00 | --- | --- | --- |
| Cobble | 21 | 16.2 | 0.33 | 0.252 | 0.203 | 0.546 |
| Gravel | 16 | 12.3 | 0.25 | 0.280 | 0.147 | 0.440 |
| Sand | 12 | 9.2 | 0.19 | 0.315 | 0.103 | 0.353 |
| Silt/clay | 18 | 13.8 | 0.29 | 0.267 | 0.169 | 0.482 |

Odds ratios, standard errors (SE), and 95% Confidence Intervals (CI) for eel substrate selection of leaf pack versus all others

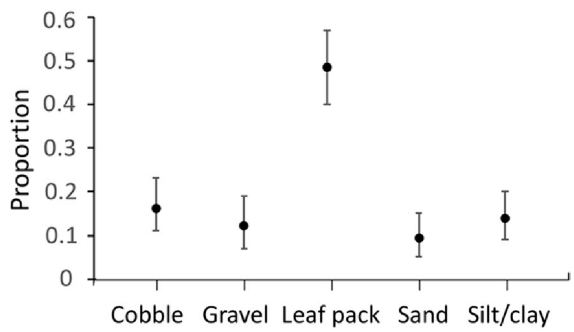


**Fig. 2** Proportions of five equally available substrate types used by yellow-phase American eels. Error bars are 95% profile likelihood confidence intervals

Angermeier 2003). Although our study also found that American eels use a wide range of substrates, leaf pack selection provides evidence for preference of a specific benthic substrate when multiple habitat types are equally available.

American eels often avoid sunlight through use of benthic substrates as burrow or refuge habitat during daytime, but also likely benefit from reduced predation risk, or increased foraging opportunities. Benthic substrates are important to yellow-phase American eels as refugia from predators (Tesch 1977; Fahay 1978; Facey and Van Den Avyle 1987). In some species, predation risk is likely reduced in substrates with adequate interstitial spaces (Stein and Magnuson 1976; Sponaugle and Lawton 1990; McAdam 2011; Smith et al. 2012). Although interstitial space is present in leaf pack habitat, its importance to the selection of leaf pack habitat in our study is unknown. American eels, however, have the ability to burrow into small-sized substrates, such as silt/clay, sand, and gravel, as well as to take refuge in substrates with larger interstitial spaces, such as leaf pack and cobble habitat. Availability of preferred habitat may reduce

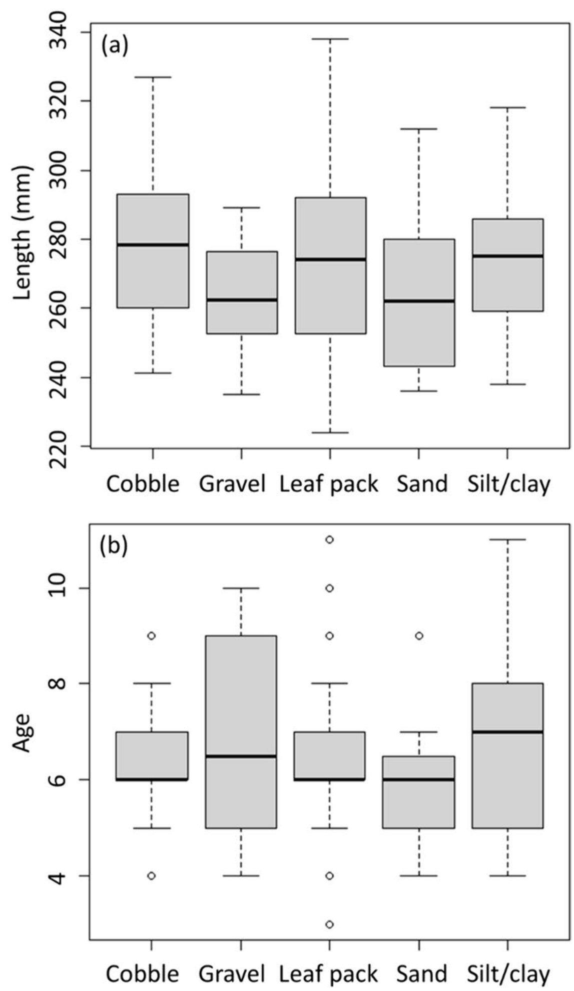


**Fig. 3** Box plot depicting American eel use of five equally available substrate types as a function of total length (a) and age (b). Bolded lines within the grey boxes are the median values, the grey boxes represent lower and upper quartile values, ends of dotted lines represent maximum and minimal values, and open circles represent outliers. Lengths ranged from 224 to 338 mm ($n=117$, mean = 273 mm, standard error = 2.34). Consensus ages ranged from 3 to 11 years ($n=117$, mean = 6 years, standard error = 0.16)

**Table 3** Deviance statistics from a multinomial logistic regression analysis assessing the influence of age and total length covariates on substrate selection by American eels

| | Df | Deviance | LR ($G^2$) | *P*-value |
|---|---|---|---|---|
| Saturated | --- | --- | --- | --- |
| Null | 12 | 331.68 | 14.50 | 0.270 |
| Age | 8 | 324.78 | 7.59 | 0.474 |
| Total length | 8 | 326.20 | 9.01 | 0.342 |
| Age + Total length | 4 | 319.04 | 1.85 | 0.763 |

predation risk, because individuals may remain in that habitat for longer periods of time and spend less time exposed to predators while searching for suitable habitat (Smith et al. 2012). Although American eels are often nocturnal foragers, food availability within benthic substrates may also influence diurnal habitat selection. Diets of small American eels consist of bottom dwelling invertebrate larvae such as Ephemeroptera, Megaloptera, and Trichoptera (Ogden 1970; Tesch 1977; Facey and LaBar 1981). Leaf packs are considered "hot spots" for invertebrate activity because they provide both substratum and nutritional resources (Hershey and Lamberti 1998). Although prey items were removed from substrates in our study, American eels may have selected leaf pack habitat because of an expectation of higher prey availability.

By using a laboratory environment, we were able to control for some of the possible biological, physical, and chemical influences that could affect the probability of selection. We realize that microhabitat selection in riverine habitat is more complicated than that represented in this controlled laboratory study, owing to other factors such as predation and food availability as previously discussed, as well as water depth and velocity, water quality, and intraspecific and interspecific competition (Krausman 1999). We also recognize differences among substrate types in an eel's ability to burrow, where compacted sand and gravel may pose more difficulty than looser substrates (Tomie et al. 2017). With exception of silt/clay substrate, we separated substrates into single categories of cobble, gravel, sand, and leaf pack; however, substrate types are often intermixed in riverine habitat. We attempted to reduce intraspecific competition through use of only five individuals per aquarium. The experimental design ensured each eel had free and equal access to all available substrate types. Results are conditional on the five experimental benthic substrates, although these substrates are present in many rivers within the North American range of the American eel.

Substrate types had equal availability during this study (a necessary design to document preference), but the availability of leaf packs may be spatially and temporally variable in aquatic systems. Leaf pack habitat occurs naturally in discrete patches. The availability of leaf pack habitat in rivers increases during late autumn and with distance upstream. During spring and summer periods of lower leaf pack availability, American eels may use a wider range of benthic substrates (Johnson and Nack 2013). Leaf pack availability is also influenced by anthropogenic factors including land use and habitat alteration, such as river channelization (Gregory et al. 1991; Schlosser 1991; Jones et al. 1999). Watershed development can reduce riparian zones and the amount of allochthonous leaves (Gregory et al. 1991; Schlosser 1991; Jones et al. 1999). River channelization removes spatial complexity and reduces structure, eddies, and slack water associated with leaf pack accumulation (Gregory et al. 1991; Schlosser 1991).

Studies have indicated that American eels use habitat differently based on body lengths (Tesch 1977; Ford and Mercer 1986; Meffe and Sheldon 1988). Size specific habitat selection also occurs in other anguillid species (Tesch 1977; Jellyman et al. 2003; Laffaille et al. 2003; Kume et al. 2020). Ford and Mercer (1986) found habitat segregation between larger and smaller American eels. During growth to larger sizes, individuals may shift from macroinvertebrate to piscivorous diets (Laffaille et al. 2003), which may be associated with shifts in habitat selection. Our study did not support size-specific habitat use, although individuals had a relatively narrow size range. In addition to size, age also did not influence substrate use. Individuals with multiple lengths and ages were often burrowed in the same leaf pack substrate bin.

Riverine habitat use reported for yellow eels from other continents may be useful for comparison with American eels given similarities among anguillid species. For example, Kumai et al. (2021) found that the Japanese eel (*Anguilla japonica*) associated with leaf litter habitat in Isso and Nagata rivers, Yakushima Island, Japan. However, Kume et al. (2020) reported that the Japanese eel used coarse substrate in the Nikkeshi River, Japan. Kumai et al. (2021) and Matsushige et al. (2022) examined habitat use of the Indo-Pacific eel (*Anguilla marmorata*), reporting an association with coarse substrates. Similarly, Degerman et al. (2019) determined that the European eel (*Anguilla anguilla*) used coarse substrates in Swedish coastal rivers. In a habitat segregation experiment conducted in New Zealand, Glova (1999) found shortfinned eels (*Anguilla australis*) associated with macrophytes and woody debris, whereas longfinned eels (*A. dieffenbachii*) used coarse substrate. The wide range of results of these studies are likely influenced by habitat availability within the natural or experimental setting. From our literature review, we realized that leaf pack habitat has often not been considered as a variable in studies of riverine habitat use of yellow eels, which may result from habitat availability or may reflect the apriori suite of variables chosen by the researchers.

In conclusion, a high percentage of yellow-phase American eels (224–338 mm TL and 3–11 years in age) selected leaf pack microhabitat during the laboratory study. If laboratory-based results are transferable to habitat use of American eels in nature, then study results support leaf pack as an important benthic habitat. Our understanding of habitat use of American eels has management and conservation implications, particularly if American eel population decline is associated with habitat loss and alterations (Castonguay et al. 1994; Haro et al. 2000). The selection preference for leaf pack habitat supports the importance of forested riparian zones to yellow-phase American eels in riverine systems.

**Acknowledgements** Funding for this study was provided by the West Virginia Division of Natural Resources and Allegheny Energy Supply. We thank Ryan Braham, Nicole Dawson, and Corbin Hilling for assistance with field collections and lab work. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of West Virginia University protocol # 11–0501.

**Data availability** Data are available from the West Virginia University data repository: https://researchrepository.wvu.edu/datasets/

**Declarations**

**Ethics approval** This study was performed under the auspices of West Virginia University IACUC protocol 11–0501.

**Competing interests** The authors declare no competing interests.

## References

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken. https://doi.org/10.1002/0471249688

ASMFC Atlantic States Marine Fisheries Commission (2000) Interstate fishery management plan for American Eel (*Anguilla rostrata*). ASMFC, Fishery Management Report 36, Washington, D.C

ASMFC Atlantic States Marine Fisheries Commission (2023) Review of the interstate fishery management plan, American Eel (*Anguilla rostrata*), 2021 fishing year. Atlantic States Marine Fisheries Commission, Washington, D.C

Bozeman EL, Helfman GS, Richardson T (1985) Population size and home range of American eels in a Georgia tidal creek. Trans Am Fish Soc 114:821–825. https://doi.org/10.1577/1548-8659(1985)114%3c821

Byers CR, Steinhorst RK, Krausman PR (1984) Clarification of a technique for analysis of utilization-availability data. J Wildl Manage 48:1050–1053. https://doi.org/10.2307/3801467

Casselman JM (2003) Dynamics of resources of the American Eel, *Anguilla rostrata*: declining abundance in the 1990s. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel biology. Springer-Verlag, Tokyo, pp 255–274

Castonguay M, Hudson PV, Couillard CM, Eckersley MJ, Dutil JD, Verreault G (1994) Why is recruitment of the American Eel, *Anguilla rostrata*, declining in the St. Lawrence River and Gulf? Can J Fish Aquat Sci 51:479–488. https://doi.org/10.1139/f94-050

Degerman E, Tamario C, Watz J, Nilsson PA, Calles O (2019) Occurrence and habitat use of European eel (*Anguilla anguilla*) in running waters: lessons for improved monitoring, habitat restoration and stocking. Aquat Ecol 53:639–650. https://doi.org/10.1007/s10452-019-09714-3

Drouineau H, Durif C, Castonguay M, Mateo M, Rochard E, Verreault G, Yokouchi K, Lambert P (2018) Freshwater eels: a symbol of the effects of global change. Fish Fish 19:903–930. https://doi.org/10.1111/faf.12300

Facey DE, Van Den Avyle MJ (1987) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (north Atlantic): American eel. U.S. Fish and Wildlife Service biological report 82(11.74). U.S. Army Corps of Engineers, TR EL-82–4

Facey DE, LaBar (1981) Biology of American eels in Lake Champlain, Vermont. T Am Fish Soc 110:396–402. https://doi.org/10.1577/1548-8659(1981)110%3c396

Fahay MP (1978) Biological and fisheries data on American eel, *Anguilla rostrata* (LeSueur). Technical series report No. 17. National Marine Fisheries Service, NOAA, Highlands, New Jersey

Ford TE, Mercer E (1986) Density, size distribution, and home range of American Eels, *Anguilla rostrata*, in a Massachusetts salt marsh. Environ Biol Fish 17:309–314

Glova GJ (1999) Cover preference tests of juvenile shortfinned eels (*Anguilla australis*) and longfinned eels (*A. dieffenbachii*)

in replicate channels. New Zeal J Mar Fresh 33:193–204. https://doi.org/10.1080/00288330.1999.9516870
Goodwin KR, Angermeier PL (2003) Demographic characteristics of American Eel in the Potomac River drainage, Virginia. Trans Am Fish Soc 132:524–535. https://doi.org/10.1577/1548-8659(2003)132%3c0524
Gregory SV, Swanson FJ, McKee WA, Cummins KW (1991) An ecosystem perspective of riparian zones. Bioscience 41:540–551. https://doi.org/10.2307/1311607
Haro AJ, Richkus W, Whalen K, Hoar A, Busch WD, Lary S, Brush T, Dixon D (2000) Population decline of the American Eel: implications for research and management. Fisheries 25(9):7–16. https://doi.org/10.1577/1548-8446(2000)025%3c0007
Hedger RD, Dodson JJ, Hatin D, Caron F, Fournier D (2010) River and estuary movements of yellow-stage American Eels *Anguilla rostrata*, using a hydrophone array. J Fish Biol 76:1294–1311. https://doi.org/10.1111/j.1095-8649.2010.02561.x
Helfman GS, Facey DE, Hales LS, Bozeman EL (1987) Reproductive ecology of the American Eel. Am Fish Soc Symp 1:42–56
Hershey AE, Lamberti GA (1998) Stream macroinvertebrate communities. In: Naiman RJ, Bilby RE (eds) River ecology and management. Springer, New York, pp 165–195
Hosmer DW, Lemeshow S (2000) Applied logistic regression. Wiley, Hoboken. https://doi.org/10.1002/0471722146
Jellyman DJ, Bonnett ML, Sykes JRE (2003) Contrasting use of daytime habitat by two species of freshwater eel *Anguilla* ssp. in New Zealand Rivers. Am Fish Soc Symp 33:63–78
Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71. https://doi.org/10.2307/1937156
Johnson JH, Nack CC (2013) Habitat use of the American eel (*Anguilla rostrata*) in a tributary of the Hudson River, New York. J Appl Ichthyol 29:1073–1079. https://doi.org/10.1111/jai.12253
Jones EBD III, Helfman GS, Harper JO, Bolstad PV (1999) Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv Biol 13:1454–1465. https://doi.org/10.1046/j.1523-1739.1999.98172.x
Krausman PR (1999) Some basic principles of habitat use. In: Launchbaugh KL, Sander KD, Mosley JC (eds) Grazing behavior of livestock and wildlife. Idaho forest, wildlife and range experimental station bulletin 70, University of Idaho, Moscow, pp 85–90
Kumai Y, Kuroki M, Morita K (2021) Influence of environmental parameters on habitat use by sympatric freshwater eels *Anguilla marmorata* and *Anguilla japonica* on Yakushima Island, Japan. Can J Zool 99:1020–1027. https://doi.org/10.1139/cjz-2021-0125
Kume M, Terashima Y, Kawai F, Kutzer A, Wada T, Yamashita Y (2020) Size-dependent changes in habitat use of Japanese eel *Anguilla japonica* during the river life stage. Environ Biol Fish 103:269–281. https://doi.org/10.1007/s10641-020-00957-w
Laffaille P, Feunteun E, Baisez A, Robinet T, Acou A, Legault A, Lek S (2003) Spatial organisation of European eel *Anguilla anguilla* in a small catchment. Ecol Freshw Fish 12:254–264. https://doi.org/10.1046/j.1600-0633.2003.00021.x
Liew PKL (1974) Age determination of American Eels based on the structure of their otoliths. In: Bagenal TB (ed) The aging of fish. Unwin Brothers, Surrey, pp 124–136
Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson EP (2002) Resource selection by animals: statistical design and analysis of field studies, 2nd edn. Kluwer Academic Publishers, Dordrechut. https://doi.org/10.1007/0-306-48151-0
Matsushige K, Yasutake Y, Mochioka N (2022) Contrasting riverine distribution and habitat use of the Japanese eel, *Anguilla japonica*, and the giant mottled eel, *Anguilla marmorata*, in a sympatric river. J Fish Biol 101:1617–1622. https://doi.org/10.1111/jfb.15224
McAdam SO (2011) Effects of substrate condition on habitat use and survival by white sturgeon (*Acipenser transmontanus*) larvae and potential implications for recruitment. Can J Fish Aquat Sci 68:812–822. https://doi.org/10.1139/f2011-021
Meffe GK, Sheldon AL (1988) The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. Am Midl Nat 120:225–240. https://doi.org/10.2307/2425994
Morrison WE, Secor DH (2003) Demographic attributes of yellow-phase American Eels (*Anguilla rostrata*) in the Hudson River estuary. Can J Fish Aquat Sci 60:1487–1501. https://doi.org/10.1139/f03-129
Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilization-availability data. J Wildl Manage 38:541–545. https://doi.org/10.2307/3800887
Ogden JC (1970) Relative abundance, food habits, and age of the American Eel, *Anguilla rostrata* LeSueur in certain New Jersey streams. Trans Am Fish Soc 99:54–59. https://doi.org/10.1577/1548-8659(1970)99%3c54
Oliveira K (1996) Field validation of annular growth rings in the American Eel, Anguilla rostrata, using tetracycline-marked otoliths. Fish B-NOAA 94:186–189
Oliveira K (1997) Movements and growth rates of yellow-phase American eels in the Annaquatucket River, Rhode Island. Trans Am Fisheries Soc 126:638–646. https://doi.org/10.1577/1548-8659(1997)126%3c0638
R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org. Accessed 5 Aug 2011
Schlosser IJ (1991) Stream fish ecology: a landscape perspective. Bioscience 41:704–712. https://doi.org/10.2307/1311765
Smith DM, Welsh SA, Turk PJ (2012) Available benthic habitat type may influence predation risk in larval lampreys. Ecol Freshw Fish 21:160–163. https://doi.org/10.1111/j.1600-0633.2011.00532.x
Smogor RA, Angermeier PL, Gaylord CK (1995) Distribution and abundance of American Eels in Virginia streams: tests of null models across spatial scales. Trans Am Fish Soc 124:789–803. https://doi.org/10.1577/1548-8659(1995)124%3c0789
Sponaugle S, Lawton P (1990) Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. Mar Ecol Prog Ser 67:43–53. https://doi.org/10.3354/meps067043
Stein RA, Magnuson JJ (1976) Behavioral response of crayfish to a fish predator. Ecology 57(4):751–761. https://doi.org/10.2307/1936188

Tesch FW (1977) The eel. Biology and management of anguillid eels. Chapman and Hall, London. https://doi.org/10.1007/978-94-009-5761-9

Tomie JP, Cairns DK, Courtenay SC (2013) How American eels *Anguilla rostrata* construct and respire in burrows. Aquat Biol 19:287–296. https://doi.org/10.3354/ab00538

Tomie JPN, Cairns DK, Hobbs RS, Desjardins M, Fletcher GL, Courtenay SC (2017) American eel (*Anguilla rostrata*) substrate selection for daytime refuge and winter thermal sanctuary. Mar Freshwater Res 68:95–105. https://doi.org/10.1071/MF15102

Welsh SA, Aldinger JL, Braham MA, Zimmerman JL (2016) Synergistic and singular effects of river discharge and lunar illumination on dam passage of upstream migrant yellow-phase American eels. ICES J Mar Sci 73:33–42. https://doi.org/10.1093/icesjms/fsv052

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392

Wiley D, Morgan RP, Hilderbrand RH (2004) Relations between physical habitat and American Eel abundance in five river basins in Maryland. Trans Am Fish Soc 133:515–526. https://doi.org/10.1577/T02-162.1

Zimmerman JL, Welsh SA (2008) PIT tag retention in small (205–370 mm) American Eels, *Anguilla rostrata*. Proc West Virginia Acad Sci 79(2):1–8