

Effect of Discharge on Daytime Habitat Use and Selection by Muskellunge in the New River, Virginia

TRAVIS O. BRENDEN,*¹ BRIAN R. MURPHY, AND ERIC M. HALLERMAN

Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0321, USA

Abstract.—For several fish species, increased river discharge has been linked to behavioral changes, including movement towards particular habitats. From 2000 to 2003, we used radiotelemetry to monitor habitat use by 42 muskellunge *Esox masquinongy* within a 17-km reach of the New River, Virginia; to evaluate habitat selection; and to determine whether habitat use and selection were affected by discharge. Water depth, occurrence of aquatic vegetation, substrate type, and distance to riverbanks within the study reach were mapped with hydroacoustic and Global Positioning System technologies. Real-time discharge measurements from an upstream U.S. Geological Survey stream gauge were used to classify fish locations into those made during periods of reduced (<75 m³/s) or increased (>75 m³/s) discharge. Seasonal habitat selection models for the different discharge levels were created using logistic regression. Differences in logistic regression coefficients between models were tested with multivariate chi-square tests and Bonferroni-corrected pairwise comparisons. Meta-analytic averaging of Pearson's correlation coefficients was used to determine the overall effect size of discharge on habitat use by muskellunge. Overall, muskellunge exhibited a positive selection for deeper habitats; however, discharge was found to significantly affect both habitat use and selection. Habitat use was consistent with the hypothesis that fish moved to shallower habitats (both summer and winter) located closer to riverbanks (winter only) during periods of increased discharge. In terms of habitat selection, selection strengths for variables such as water depth (summer and winter) and distance to shoreline (winter only) generally weakened during periods of increased discharge, indicating that habitat use became more proportionate to availability. Increased movement as a result of increased discharge has been theorized to potentially reduce winter survival of fish because of seasonal energetic limitations. Thus, indirect effects on fish from dam operating modes (e.g., hydropeaking) may be as important as direct effects when evaluating biotic implications of water release schedules.

The muskellunge *Esox masquinongy* is a primarily piscivorous fish species having a native range restricted to the Mississippi, Ohio, St. Lawrence, and Tennessee River drainages of North America (Crossman 1978). Due to its popularity as a sport fish, though, the muskellunge has been introduced throughout North America (Crossman 1986). In the southeastern United States, the muskellunge has been introduced to water bodies in Alabama, Arkansas, Georgia, Kentucky, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia (USGS 2004a). Some of the most productive muskellunge fisheries resulting from these introductions have been in riverine environments due possibly to factors such as greater food availability (Harrison and Hadley 1979) or cooler water temperatures. In Virginia, the top trophy-producing muskellunge fisheries (trophy muskellunge size in Virginia is designated as $\geq 1,016$ mm or ≥ 6.8 kg) have been the

New and James rivers. From 1990 to 2003, these rivers produced 58% ($n = 546$) of trophy muskellunge registered with Virginia's Angler Recognition Program, the remaining number divided among 20 other lakes, reservoirs, and rivers (Virginia Department of Game and Inland Fisheries [VDGIF], unpublished data).

Despite the recreational opportunities provided by riverine muskellunge fisheries in the southeastern United States, very little regional research related to muskellunge biology and ecology in rivers has been conducted. The only information regarding muskellunge habitat use in southeastern U.S. rivers comes from descriptions of fish sampling locations (Parsons 1959; Miles 1978; Brewer 1980; Axon and Kornman 1986; Monaghan and Borawa 1988). The ability to link such descriptions to actual habitat selection, though, is premised on sampling being equally effective across habitat types, an assumption that rarely is met. Boat electrofishing, which often is used to sample muskellunge in rivers (Miles 1978; Axon and Kornman 1986; Monaghan and Borawa 1988), is generally effective over a limited range of water depths (Reynolds 1996). Electrofishing also is often conducted exclusively along riverbanks; thus, it may not be known to what

* Corresponding author: brenden@msu.edu

¹ Present address: Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824-1222, USA.

extent midchannel habitats are used. Although research into muskellunge habitat use and selection in both riverine and lacustrine environments has been more frequently conducted in northern U.S. regions (Dombeck et al. 1984; Miller and Menzel 1986a; Farrell et al. 1996; Younk et al. 1996), questions regarding transferability of results limits applicability of these findings to southeastern U.S. systems (Leftwich et al. 1997).

One factor that may be particularly important to muskellunge habitat use and selection in rivers is discharge. Increased discharge has been linked to changes in fish behavior in several species, including movement towards particular habitats (Kwak 1988; Todd and Rabeni 1989; Matheney and Rabeni 1995; Harvey et al. 1999; Muhlfeld and Marotz 2005); however, we are unaware of any prior research linking changes in discharge to changes in muskellunge habitat use or selection. If habitat use or selection changes with discharge, identification of habitat requirements for the species will be complicated if discharge is excluded from analyses. For example, if fish select deeper areas during periods of reduced discharge and shallower areas during periods of increased discharge, the interaction with discharge could negate an overall water depth effect. Understanding how muskellunge habitat use and selection changes with discharge also may be beneficial to management by aiding in the identification of suitable stocking sites. Fish that are stocked in sections of rivers that do not meet habitat requirements during periods of increased discharge may move or be displaced to other areas (Moog 1993). Given the controversy that sometimes surround the stocking of esocids due to possible predatory impacts on prey fish populations (Siler and Beyerle 1986; Moyle 2002), volitional movement or displacement of fish could result in a significant dilemma for fishery managers. The purpose of this study was to describe muskellunge habitat selection and to determine whether changes in discharge significantly affected muskellunge habitat use and selection in the New River, Virginia.

Study Site

The New River originates in northwest North Carolina and flows northward through southwest Virginia and into West Virginia (Figure 1). The river basin lies within two Virginia physiographic provinces, the Southeastern Blue Ridge Mountain and Ridge and Valley provinces. The New River merges with the Gauley River near Anstead, West Virginia, to form the Kanawha River, which is a tributary to the Ohio River.

Compared with other Virginia drainages, the New River has a low number of native fish species (Jenkins

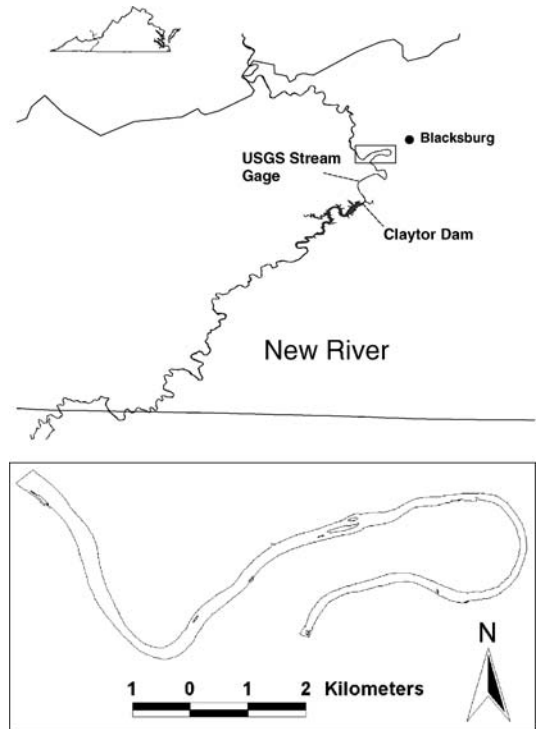


FIGURE 1.—The 17-km study reach and its location in the New River, Virginia, where muskellunge were tracked by radiotelemetry to determine their habitat use.

and Burkhead 1993). Forty-six species are believed to be native to the New River drainage; 42 other species have been introduced (Jenkins and Burkhead 1993). Muskellunge, which are not believed to be native to the New River (Jenkins and Burkhead 1993), have been stocked by VDGIF on an approximately annual basis since the 1960s (J. Williams, VDGIF, personal communication).

Our research was conducted within a section of the New River near Blacksburg, Virginia (Figure 1). This river section was selected because it offered a variety of habitats and because it was one of the longest stretches on the river that was accessible by boat even during periods of reduced discharge. The study area was 17 river kilometers (rkm) long, having a total surface area of approximately 300 ha. Discharge in this section of the river is regulated primarily by Clayton Hydroelectric Dam (Figure 1). Mean annual discharge for this section of the New River is approximately 100 m³/s (USGS 2004b).

Methods

Transmitter implantation and tracking methodology.—Forty-two muskellunge ranging in total length

from 655 to 1,256 mm were collected by boat electrofishing ($n = 36$) and angling ($n = 6$) from early winter to late spring in 2000 ($n = 15$), 2001 ($n = 13$), and 2002 ($n = 14$). Radiotelemetry transmitters (Advanced Telemetry Systems, Isanti, Minnesota) operating in the 48–50-mHz bandwidth range were surgically inserted into the peritoneum of each fish through incisions made proximate to the midventral line and posterior to the pelvic girdle. Surgical staples were used to close the incisions for the first few fish implanted with transmitters, but we later switched to nonabsorbable sutures as staples sometimes tore through incision margins in large fish. Fish were returned to the river upon completion of the surgery, restrained until equilibrium was regained, and then released. Transmitter mass ranged from 28 to 90 g, and transmitters weighed $1.03 \pm 0.12\%$ (mean \pm 2SE) of fish body weight. Expected transmitter battery life ranged from 500 to 1,100 d.

Weekly tracking of telemetered fish began 1 June 2000 and continued until 11 June 2003. Occasionally, poor weather conditions or equipment failure resulted in tracking not being conducted in a particular week. Tracking was conducted only during daylight hours because of difficulties in searching the study reach at night due to exposed areas of bedrock. Time of day that tracking began and the route that was used to search the study reach (i.e., upstream from furthest downstream point, downstream from furthest upstream point, upstream from study reach midpoint then downstream, downstream from study reach midpoint then upstream) typically varied between tracking events to prevent fish from being located at similar times of the day across tracking events. Tracking began at between 0500 and 1600 hours and typically was completed by 2000 hours. Fish were tracked from a boat by homing with an R2000 receiver (Advanced Telemetry Systems) and a loop antenna. As fish positions were approached, the loop antenna was disconnected and only the exposed end of a coaxial cable was used to pinpoint fish locations. Fish locations were recorded with Global Positioning System (GPS) receivers. So as not to bias descriptions of used habitats, we discontinued tracking if it became apparent that fish possibly were moving as a result of the tracking process. Distance error in locating and mapping transmitter position using these methods and equipment ranged from 1 to 15 m in a previous assessment (Brenden et al. 2004).

Habitat measurement and mapping.—We used hydroacoustics to measure water depth, occurrence of aquatic vegetation, and substrate type within the study reach. Sampling was conducted with a DE Series 4000 echosounder and a 430-kHz single-beam 6.2° transducer (Biosonics, Inc., Seattle, Washington). Hydro-

acoustic measurements were georeferenced through a differentially corrected GPS receiver. Sampling was conducted along virtual transects (that ran parallel to the riverbanks) created in ArcView GIS software (ESRI, Redlands, California). Distance between transects was 5 m when measuring water depth and aquatic vegetation and 25 m when measuring substrate type. Transect locations were uploaded to a GPS receiver, which was used to display boat and transect locations in real time. Hydroacoustic sampling of water depth and aquatic vegetation was performed with a -130 -dB noise threshold at a pulse rate of 10 pings/s and a pulse width of 0.3 ms. Sampling of substrate was performed with a -70 -dB noise threshold at a pulse rate of 5 pings/s and a pulse width of 0.1 ms. Hydroacoustic sampling generally could only be conducted at discharges below $100 \text{ m}^3/\text{s}$ because of interference of hydroacoustic echoes at greater discharges. Thus, evaluations of habitat use and selection between discharge levels were made relative to a baseline (reduced discharge) habitat map.

Hydroacoustic data were processed with EcoSAV and Visual Bottom Typing Seabed Classification (VBTSC) software (Biosonics). We used EcoSAV to estimate water depth and occurrence of aquatic vegetation, while VBTSC was used to identify substrate type. For this research, we classified substrate into one of three types: bedrock–boulder, gravel–cobble, and sand–mud. A training data set for the identification of substrate type was created by sampling areas in the study reach consisting primarily of these substrate types. A total of 20 transects (number of transects: six bedrock–boulder, seven gravel–cobble, seven sand–mud) were sampled in creating this training data set. After processing the training data with VBTSC, discriminant analysis was used to find a linear combination of the digital echo characteristics that best distinguished among the three substrate types. The resulting discriminant function was then used to classify substrate type across the entire study reach. Mean cross validation accuracy in identifying substrate type for the training data was 87% (Table 1).

Bathymetric and aquatic vegetation maps for the study reach were created with inverse-distance weighting interpolation. A substrate-type map for the study reach was created by overlaying a blank 25-m pixel grid across the study reach and then assigning to the cells the most frequently occurring substrate type. For example, if a grid cell overlay five sand–mud observations and one cobble–gravel observation, then that cell was assigned a sand–mud substrate type.

Real-time discharges during the time period that muskellunge tracking was conducted were obtained from the USGS New River stream gauge at Radford,

TABLE 1.—Cross-validation classification accuracies for identifying substrate type for the reference hydroacoustic database from discriminant analysis. Cells along the diagonal are the percent of substrate types correctly classified. Off-diagonal cells are the percent of substrate types incorrectly classified.

True substrate type	Classified substrate type		
	Bedrock–boulder	Gravel–cobble	Sand–mud
Bedrock–boulder	86.4	13.6	0.0
Gravel–cobble	0.0	90.2	9.8
Sand–mud	0.4	13.4	86.2

Virginia (USGS 2004b). From the stream gauge data, we calculated median discharge for the 12 h prior to the muskellunge locations. Because the stream gauge is located several kilometers upstream from the study reach (Figure 1), we assumed that it would take an average of 7 h before the discharge measured at the stream gauge reached the study reach (American Electric Power, unpublished data). For example, if a fish was located at 1400 hours on a Friday, median discharge was calculated from the stream gauge data from 1900 hours on Thursday to 0700 hours on Friday.

Verification of habitat map accuracy.—We verified accuracy of the bathymetric, aquatic vegetation, and substrate-type maps by field-measuring habitat conditions at approximately 300 locations within the study reach. Locations where field measurements were taken were randomly assigned in ArcView GIS. Water depth was measured with a stadia rod or an SM-5 Depthmate portable sounder (Speedtech Instruments, Great Falls, Virginia). Presence of aquatic vegetation was determined visually or through a modified rake technique (Brenden 2005). Substrate type was identified by probing the river bottom with a piece of aluminum conduit and classifying substrates based on penetration depth and texture.

We used ArcView GIS to estimate mean water depth, occurrence of aquatic vegetation, and predominant substrate type within 10-m-radius buffers surrounding the random locations based on the delineated habitat maps. We then compared these GIS estimates of habitat condition to field measurements. Although the comparison of field-measured and GIS-derived estimates indicated that bathymetric and aquatic vegetation maps were accurate, accuracy of the substrate-type map was found to be poor. Absolute deviation of mapped from field-measured water depths was 0.21 ± 0.03 m (mean \pm 2SE), and 83% of locations were correctly classified in terms of aquatic vegetation occurrence. Conversely, only 38% of locations were correctly classified in terms of substrate type. Although reducing

the classification to fine and coarse substrate types increased classification accuracy to 56%, we still considered this too low to include this variable in subsequent analyses and thus substrate type was excluded from all models.

Habitat selection pooled across discharge levels.—Muskellunge habitat selection pooled across discharge levels was initially assessed through a Design III study, meaning that habitat use and availability were compared for individual fish (Thomas and Taylor 1990; Manly et al. 2002). Comparisons of use and availability were limited to locations occurring within fish home ranges (third-order selection; Johnson 1980). Summer and winter 90% probabilistic home ranges were delineated in S-Plus (Mathsoft 1999) using Vokoun's (2003) kernel density approach and a Gaussian density function. Bandwidths were determined through unbiased cross validation (Venables and Ripley 1997). Home ranges were delineated only for fish that were located at least 30 times in a season, which was the minimum sample size recommended by Vokoun (2003). Time frames for delineating summer and winter home ranges were determined for each fish individually (Brenden 2005).

Habitat use was measured by buffering all fish locations that occurred within the boundaries of a fish's home range with 10-m-radius circles. Mean water depth within the buffered fish locations and nearest distances of the buffered fish locations to the riverbank, to an aquatic vegetation patch greater than 50 m² (summer only), and to the depth contours of 0–1, 1–2, 2–3, 3–4, and 4–5-m were calculated in ArcView GIS. A 10-m radius was chosen for buffering the fish locations as a prior accuracy assessment indicated that nearly 99% of all tracking errors occurred within this distance (Brenden et al. 2004).

Habitat availability within fish home ranges was measured by first creating a 20-m pixel grid that covered the entire study reach. The centroids of the grid cells were then identified and buffered with 10-m-radius circles, which resulted in a layer of nonoverlapping circular features (availability circles). We then used ArcView GIS to calculate mean water depths and nearest distances to the riverbank, to an aquatic vegetation patch greater than 50 m² in area (summer only), and to the 0–1-, 1–2-, 2–3-, 3–4-, and 4–5-m depth contours for the availability circles. We then clipped the layer of availability circles to the spatial extent of each fish's home range.

Seasonal habitat selection models were created with logistic regression by modeling used and available locations as functions of their habitat attributes (Manly et al. 2002). Habitat selection models were fit only for fish that had a minimum of 25 locations within their

home range for a particular season. Logistic regression models were fit to all possible combinations of variables, and model averaging based on Akaike's information criterion corrected for small sample size (AIC_c) was used to develop coefficient estimates for the habitat attributes included in the selection models (Anderson et al. 2000). Only models with evidence ratios greater than one-eighth when compared with that of the model with the lowest AIC_c value were included in the model-averaging process (Thompson and Lee 2002). We then averaged model coefficient estimates across all telemetered fish as a means for inferring habitat selection to a larger segment of the New River muskellunge population (Erickson et al. 2001). We tested whether model coefficients for the summer and winter habitat selection models were significantly different from zero with Wilcoxon's signed rank tests. Differences in model coefficients between seasons were tested with two-sample Wilcoxon rank-sum tests.

Effect of discharge on muskellunge habitat use and selection.—The effect of discharge on muskellunge habitat use was assessed through Pearson's correlations of river discharge in relation to habitat attributes of buffered fish locations. Correlations were calculated separately for locations occurring from 1 April to 15 November (summer) and 16 November to 31 March (winter). Correlations were only calculated for fish with at least 25 location estimates for these time periods. The cutoff dates for these time periods correspond approximately to when water temperature in the New River approaches 10°C (T. O. Brenden, unpublished data), which Minor and Crossman (1978) found was the approximate temperature that muskellunge started transitioning between home ranges.

After correlating habitat attributes of used locations with discharge measurements, we then used a meta-analytic approach for combining correlation coefficients to determine the overall effect size of river discharge on habitat use (Hedges and Olkin 1985). This involved normalizing correlation coefficients using the Fisher's Z -transformation and calculating weighted averages and standard errors of the transformed coefficients based on the numbers of fish locations (Hedges and Olkin 1985). Overall Z -transformed effect sizes of river discharge on habitat attribute use were calculated by dividing the weighted averages of the transformed correlation coefficients by their standard errors (Hedges and Olkin 1985). Statistical significance of effect sizes were tested with standard normal tests.

The effect of discharge on muskellunge habitat selection was evaluated by pooling telemetered fish locations into seasonal data sets (based on the same time periods used for correlating discharge with habitat use) and modeling selection in relation to habitat

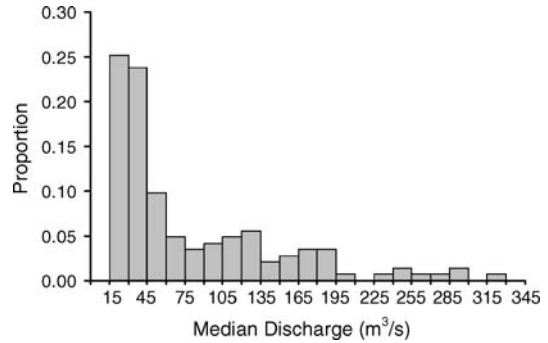


FIGURE 2.—Frequency histogram of median river discharge measurements for 12 h prior to each location estimate made for radio-tagged muskellunge in the New River, Virginia. Locations associated with high and low discharges were classified based on the overall mean (75 m³/s) of the discharge measurements.

availability across the entire study reach (Design I study; Thomas and Taylor 1990; Manly et al. 2002). Each fish location was classified as to whether it was made during a period of increased or reduced discharge, distinguished based on the frequency distribution of median river discharge estimates for the fish relocations. Reduced discharge locations were those made when discharge was less than the mean of the discharge estimates (mean = 75 m³/s), while increased discharge locations were those made when discharge was greater than the mean of the discharge estimates (Figure 2).

Winter and summer habitat selection models for locations made during periods of increased and reduced discharges were fit with logistic regression. We then used the approach of Allredge and Dasgupta (2003) to test if coefficients significantly differed between discharge levels. This involved initially testing whether an overall difference in model coefficients existed among the discharge levels through multivariate chi-square tests. If a significant overall difference in model coefficients was found, we then tested individual model coefficients for differences between the discharge levels (Allredge and Dasgupta 2003). When testing coefficients between models, we used Holm's (1979) stepdown Bonferroni method to protect the type I error rate of the tests (Allredge and Dasgupta 2003). Unless otherwise noted, statistical tests were conducted in SAS (SAS Institute 2004) at an α equal to 0.05.

Results

The total number of locations for muskellunge equipped with transmitters ranged from 3 to 141 (mean \pm 2SE = 43 \pm 11 locations). The number of elapsed days between date of transmitter implantation and date

TABLE 2.—Model-average coefficients (mean \pm 2SE) for habitat variables included in seasonal habitat selection models for muskellunge in the New River, Virginia. Also shown are the Wilcoxon signed-rank test statistics (S) and P -values for testing the hypotheses that the coefficients are significantly different from zero. The number of telemetered muskellunge used for each model is indicated in parentheses; NA indicates that the variable was not included in the analysis.

Model parameter	Winter ($n = 6$)			Summer ($n = 17$)		
	Estimate \pm 2SE	S	P	Estimate \pm 2SE	S	P
Mean depth (m)	0.950 \pm 0.413	10.5	0.003	0.890 \pm 0.313	75.5	<0.001
Distance to riverbank (m)	0.004 \pm 0.007	1.5	0.844	0.004 \pm 0.013	19.5	0.378
Aquatic vegetation	NA	NA	NA	-0.003 \pm 0.004	-32.5	0.132
Depth contour						
0-1 m	0.000 \pm 0.007	-1.5	0.844	0.012 \pm 0.020	30.5	0.159
1-2 m	-0.001 \pm 0.013	-2.5	0.687	-0.007 \pm 0.016	-15.5	0.487
2-3 m	-0.017 \pm 0.028	-4.5	0.437	-0.014 \pm 0.019	-54.5	0.008
3-4 m	-0.021 \pm 0.033	-9.5	0.062	-0.006 \pm 0.015	-31.5	0.145
4-5 m	0.004 \pm 0.006	4.5	0.437	-0.000 \pm 0.004	-17.5	0.431

of last location ranged from 28 to 1,176 d (mean \pm 2SE = 423 \pm 90 d). Individual home ranges and habitat selection models were created for 6 and 17 fish for winter and summer, respectively. The lengths of fish for which individual habitat selection models were created ranged from 730 to 965 mm for winter and from 682 to 1,020 mm for summer. Habitat use and selection in relation to discharge were evaluated through pooling locations from among 9 muskellunge for winter and 20 muskellunge for summer. Lengths of fish ranged from 682 to 1,020 mm for the discharge-related analyses.

Of the 42 muskellunge initially equipped with transmitters, 7 fish had operable transmitters and were located in the study reach when the study ended. Of the other 35 fish, 7 were occupying sites outside the study reach; 5 had been harvested by anglers; 3 had experienced natural, postsurgical, or post-angler release mortality; 1 was euthanized after it was recaptured and found to have an infection at the incision site; and 1 had a transmitter that malfunctioned. The fates of the remaining 18 fish are unknown, although it is likely that the transmitters from seven of the fish stopped functioning due to expended batteries.

Habitat Selection Pooled across Discharge Levels

During winter, mean depth was the only habitat variable included in the individual habitat selection models that was significantly different from zero ($\beta = 0.950$; $S = 10.5$; $P = 0.003$). The sign of the coefficient for mean depth was positive, indicating that muskellunge selected locations that were deeper than what would be expected based on habitat availability. Significant differences in coefficients from zero for the other habitat variables were not detectable at α equal to 0.05 (Table 2), indicating that habitat use was proportional to that of availability. We used simple

linear regression to relate fish lengths to model-average coefficients as a way of determining whether habitat selection changed with fish size. Slopes for these regressions, however, were not significantly different from zero ($P \geq 0.29$); thus, we do not believe that habitat selection was a function of fish length.

During summer, mean depth and nearest distance to the 2-3-m depth contour were the only habitat variables with model coefficients that were significantly different from zero (mean depth: $\beta = 0.890$, $S = 75.5$, $P < 0.001$; distance to 2-3-m depth contour: $\beta = -0.014$, $S = -54.5$, $P = 0.008$). As was found during winter, the sign of the coefficient for mean depth was positive, indicating that muskellunge positively selected deeper habitats. The sign of the coefficient for nearest distance to the 2-3-m depth contour was negative, indicating that muskellunge selected locations closer to areas of this depth than what would be expected based on habitat availability. Significant differences in coefficients from zero for the other habitat variables were not detectable at α equal to 0.05 (Table 2), indicating that habitat use was comparable to that of availability. As in winter, slopes of simple linear regressions of model-average coefficients versus fish lengths were not significant ($P > 0.25$). No significant differences between summer and winter model coefficients were detected, indicating that patterns in habitat selection remained similar between seasons (Table 3).

Effect of Discharge on Habitat Use and Selection

During winter, river discharge was found to have a statistically significant effect on use of all habitat variables. Mean depth, nearest distance to the riverbank, and nearest distances to the 0-1- and 1-2-m depth contours had negative relationships with river discharge, while nearest distances to the 2-3-, 3-4-, and 4-5-m depth contours had positive relationships

TABLE 3.—Wilcoxon rank-sum test statistics (*W*) and *P*-values for testing differences in coefficients between winter and summer muskellunge habitat selection models for the New River, Virginia.

Model parameter	<i>W</i>	<i>P</i>
Mean depth (m)	198	0.700
Distance to riverbank (m)	208	0.806
Depth contour		
0–1 m	219	0.310
1–2 m	202	0.916
2–3 m	194	0.506
3–4 m	219	0.310
4–5 m	186	0.221

(Table 4). During summer, nearest distances to the riverbank and to an aquatic vegetation patch greater than 50 m² were the only habitat variables not significantly affected by discharge (Table 4). For those summer habitat variables that were significantly affected by discharge, effects were similar in direction to those observed in winter. Winter effects generally were greater in magnitude than the effects observed in summer, indicating that habitat use was more strongly affected by discharge during the winter than in summer.

An overall significant difference in coefficients was detected between habitat selection models constructed for periods of increased and reduced discharges during winter (Wald chi-square = 156.78; *P* < 0.001). Testing of individual model coefficients indicated that coefficients corresponding to mean depth (*Z* = 5.45; Bonferroni-adjusted *P* < 0.001), nearest distance to the riverbank (*Z* = 3.16; Bonferroni-adjusted *P* = 0.008), nearest distance to the 2–3-m depth contour (*Z* = -3.27; Bonferroni-adjusted *P* = 0.006), and nearest distance to the 4–5-m depth contour (*Z* = -2.95; Bonferroni-adjusted *P* = 0.022) significantly differed between periods of increased and reduced discharges. During periods of increased discharge, selection strengths for these habitat variables generally declined

(Table 5), although in no instance did selection for a particular habitat variable change from a significant positive to a significant negative selection (or vice versa). Rather, selection for the habitat variables remained either significantly positive, as was the case for mean depth, or changed from a significantly positive or negative selection to neutral selection, as was the case for nearest distance to the riverbank and nearest distances to the 2–3- and 4–5-m depth contours (Table 5).

An overall significant difference in model coefficients was detected between habitat selection models constructed for periods of increased and reduced discharges during the summer as well (Wald chi-square = 457.30; *P* < 0.001). Only the coefficients for mean depth were significantly different between the discharge levels (*Z* = 7.37; Bonferroni-corrected *P* < 0.001). Selection for locations based on mean depth was significantly positive for both periods of increased and reduced discharges, although the strength of selection did decrease during periods of increased discharge (Table 5).

Discussion

Prior studies of adult muskellunge habitat use have found fish during the summer to occupy well-defined home ranges and to use areas less than 2 m deep with high densities of logs or tree stumps, fish often being suspended above or located between patches of aquatic vegetation (Minor and Crossman 1978; Axon and Korman 1986; Miller and Menzel 1986a; Younk et al. 1996). As water temperature drops and aquatic vegetation densities decline during fall, muskellunge abandon home ranges and become transient (Minor and Crossman 1978; Miller and Menzel 1986b). With the onset of winter, muskellunge again establish well-defined home ranges (Minor and Crossman 1978; Younk et al. 1996). Areas used in the winter tend to be

TABLE 4.—Weighted-average correlation coefficients (*r*) for the association between river discharge and muskellunge use of various habitat variables in the New River, Virginia. The standardized mean effect sizes (*Z*) and *P*-values for testing the hypotheses that the *Z*-values were significantly different from zero also are shown. The number of telemetered muskellunge used for each analysis is indicated in parentheses; NA indicates that the variable was not included in the analysis.

Model coefficient	Winter (<i>n</i> = 9)			Summer (<i>n</i> = 20)		
	<i>r</i>	<i>Z</i>	<i>P</i>	<i>r</i>	<i>Z</i>	<i>P</i>
Mean depth (m)	-0.409	-7.60	<0.001	-0.192	-5.70	<0.001
Distance to riverbank (m)	-0.225	-4.02	<0.001	-0.040	-1.17	0.244
Vegetation patch (>50 m ²)	NA	NA	NA	0.055	1.62	0.106
Depth contour						
0–1 m	-0.258	-4.62	<0.001	-0.109	-3.23	0.001
1–2 m	-0.185	-3.27	0.001	-0.075	-2.19	0.028
2–3 m	0.224	3.99	<0.001	0.133	3.92	<0.001
3–4 m	0.308	5.57	<0.001	0.116	3.43	0.001
4–5 m	0.263	4.71	<0.001	0.095	2.80	0.005

TABLE 5.—Parameter coefficients corresponding to low (β_L) and high (β_H) discharges for habitat variables included in pooled seasonal habitat selection models for muskellunge in the New River, Virginia. Coefficients marked with an asterisk were significantly different from zero ($P < 0.05$). Standard normal test statistics (Z), P -values, and stepdown Bonferroni adjusted P -values for testing differences in model coefficients for low and high discharges also are shown.

Parameter	β_L	β_H	Z	P	Adjusted P
Winter					
Mean depth (m)	0.935*	0.496*	5.45	<0.001	<0.001
Distance to riverbank (m)	0.009*	-0.005	3.16	0.002	0.008
Depth contour					
0-1 m	-0.005	0.001	-0.94	0.350	1.000
1-2 m	0.001	0.002	-0.17	0.865	1.000
2-3 m	-0.016	0.001	-3.27	0.001	0.006
3-4 m	-0.010*	-0.008*	-0.60	0.547	1.000
4-5 m	-0.001*	0.000	-2.78	0.005	0.022
Summer					
Mean depth (m)	0.924*	0.405*	7.37	<0.001	<0.001
Vegetation patch (>50m ²)	-0.001	0.001	-1.95	0.052	0.259
Distance to riverbank (m)	0.012*	0.008*	1.92	0.055	0.259
Depth contour					
0-1 m	0.001	0.000	0.20	0.839	1.000
1-2 m	-0.022*	-0.021*	-0.11	0.914	1.000
2-3 m	-0.019*	-0.010*	-2.67	0.008	0.053
3-4 m	-0.003*	-0.004*	1.14	0.255	0.764
4-5 m	0.001*	0.001*	2.36	0.018	0.110

deeper than areas used during the summer but still often are adjacent to vegetated areas (Minor and Crossman 1978). As water temperature rises in the spring, muskellunge abandon winter home ranges and begin moving to spawning areas (Minor and Crossman 1978; Miller and Menzel 1986a). Muskellunge spawning generally occurs in areas less than 1 m deep over substrates consisting of mud, silt, sand, or decomposing vegetation (Dombeck et al. 1984; Strand 1986; Farrell et al. 1996; LaPan et al. 1996; Younk et al. 1996).

In the present study, muskellunge positively selected deeper areas; however, we did find that discharge affected both habitat use and selection. Because habitat availability could not be explicitly measured at high discharges due to reception interference of the hydro-acoustic echoes, we cannot conclude with certainty to what particular habitats fish moved. However, we found no evidence to suggest that fish moved to deeper habitats as discharge increased. Rather, our results were more consistent with the hypothesis that fish moved to shallower habitats located closer to the shoreline. Because habitat availability also would have changed as discharge increased, it is possible that fish could have moved to areas that had similar habitat attributes (e.g., depth, distance to shoreline) to areas that were used at low discharges; however, this too could be interpreted as a behavioral response to changes in discharge. Selection strengths for habitat variables included in the pooled habitat selection models generally weakened as discharge increased, indicating

that habitat use became more proportionate to habitat availability with increasing discharge.

Behavioral responses of fish to changes in discharge, including movement towards particular types of habitat, have frequently been observed in research studies (Harvey et al. 1999; Dare et al. 2002; Scruton et al. 2002; Muhlfeld and Marotz 2005). Fish have been observed moving closer to riverbanks during periods of increased discharge (Kwak 1988; Todd and Rabeni 1989; Matheney and Rabeni 1995; Bunt et al. 1999; Muhlfeld and Marotz 2005), although movement to deeper water also has been observed (Scruton et al. 2002). Possible reasons why muskellunge would move into shallower areas located closer to riverbanks include seeking refuge from faster water velocities or following prey items that are attempting to escape faster water velocities. Northern hog suckers *Hypentelium nigricans*, which are important diet items for muskellunge both in the New River (Brenden et al. 2005) and elsewhere (Bozek et al. 1999), have been observed moving towards riverbanks with higher discharges (Matheney and Rabeni 1995). It thus certainly seems possible that muskellunge may move towards riverbanks during periods of increased discharge as a result of prey movement. Whether muskellunge can successfully forage during periods of increased discharge remains unknown, though. Muskellunge rely on both sight and the lateral line system when foraging; sight primarily influences initial orientation to prey, and the lateral line system plays the critical role in final capture of prey (New et al. 2001).

Blinded muskellunge can be as effective at catching prey as sighted fish (New et al. 2001), thus increased turbidity resulting from increased discharge may not hamper muskellunge foraging. Rather, increased turbidity could possibly assist muskellunge foraging if prey species rely on vision to identify and avoid potential predators. Experimentation to quantify station-holding energetic requirement and foraging success of muskellunge during periods of reduced and increased discharges would prove useful for identifying which of these hypotheses offer a more likely explanation as to why fish move into shallower areas located closer to the riverbanks during periods of increased discharge.

Our finding of a stronger effect of discharge on muskellunge habitat use and selection during the winter likely was due, in part, to differences in water release schedules from Claytor Hydroelectric Dam during the year. From approximately mid-May to mid-October, the dam is operated on a "run-of-river" release schedule in order to protect centrarchid spawning habitat in the upstream reservoir. During the rest of the year, the dam is operated on a hydropeaking release schedule (J. Williams, personal communication). Substantial differences in river discharge result from these different operation modes, fish during the winter experiencing more frequent and greater fluctuations in discharge (Figure 3) that conceivably could have led to a stronger discharge effect size during winter than in summer. Scruton et al. (2005) theorized that hydropeaking operations during the winter could have serious repercussions on fish populations given that winter is often when energy reserves in fish are depleted, and the energetic costs of moving to new habitat could decrease fish survival rates. Again, experimentation as to the energetic costs of increased discharge would be helpful in determining the overall impact of hydropeaking operations on muskellunge populations.

The lack of selection for aquatic vegetation by muskellunge in this study contradicted research findings from most habitat-related studies that have been conducted on muskellunge. For young muskellunge, aquatic vegetation is believed to attract prey and provide cover from predators (Bry 1996). For adult muskellunge, vegetation can serve as spawning substrate and as cover from which to ambush prey (Casselmann 1996). The lack of selection for aquatic vegetation in this research could stem from one of several factors. First, the importance of aquatic vegetation as foraging cover for adult muskellunge in rivers could be reduced if discharge is the major factor controlling the spatial distribution of prey items. If prey items are spatially distributed based on river discharge,

then muskellunge foraging in rivers may be concentrated around habitats that afford better cover from discharge, such as logjams or large boulders.

The scale at which we conducted our research also could explain why we did not observe muskellunge positively selecting vegetated habitats. We analyzed selection based on nearest distances to aquatic vegetations patches greater than 50 m². We did not believe that basing selection on smaller patches would be appropriate given the spacing of transects during hydroacoustic sampling. While muskellunge did not positively select these vegetated areas, fish still could select vegetated areas at smaller scales. Ambushing of prey, which is the feeding strategy employed by muskellunge (Webb and Skadsden 1980), may only require a vegetated patch a few square meters in area. Delineating habitat patches that small across spatially extensive regions may not be possible with hydroacoustics; thus, the results of this research may best be viewed as a meso- or macroscale selection of habitat. Addressing muskellunge microscale selection of habitats, such as small aquatic vegetation patches or logjams, in warmwater rivers may be best accomplished through direct, underwater observation of fish habitat use (Beauchamp et al. 1994; Walters and Wilson 1996; Baigún 2003).

Our inability to include substrate as a habitat attribute in our selection models was unfortunate as previous research has identified substrate type as an important attribute affecting muskellunge habitat use, particularly during spawning periods (Dombeck et al. 1984; Strand 1986; LaPan et al. 1996). Habitats consisting of particular substrates also may offer some protection from faster water velocities (Hayes and Jowett 1994; Crowder and Diplas 2000); thus, inclusion of substrate type in habitat selection models could have explained additional differences in habitat selection models for the different discharge levels. The high cross validation accuracy in distinguishing substrate types that was observed for the training data set, combined with the low classification accuracy for randomly assessed locations, suggests that our training data set was inadequate for delineating the full range of substrate types found in the study reach. In particular, qualitative examination of delineated substrate maps indicated that mapping accuracy was related to water depth. Shallow bedrock-boulder habitats appeared to have frequently been misclassified as gravel-cobble habitats. Similarly, shallow gravel-cobble habitat appeared to have frequently been misclassified as sand-mud habitats. Such misclassification between substrate types suggests there was potential overlap in the digital echo characteristics of substrate type at different water depths. This would make it difficult to

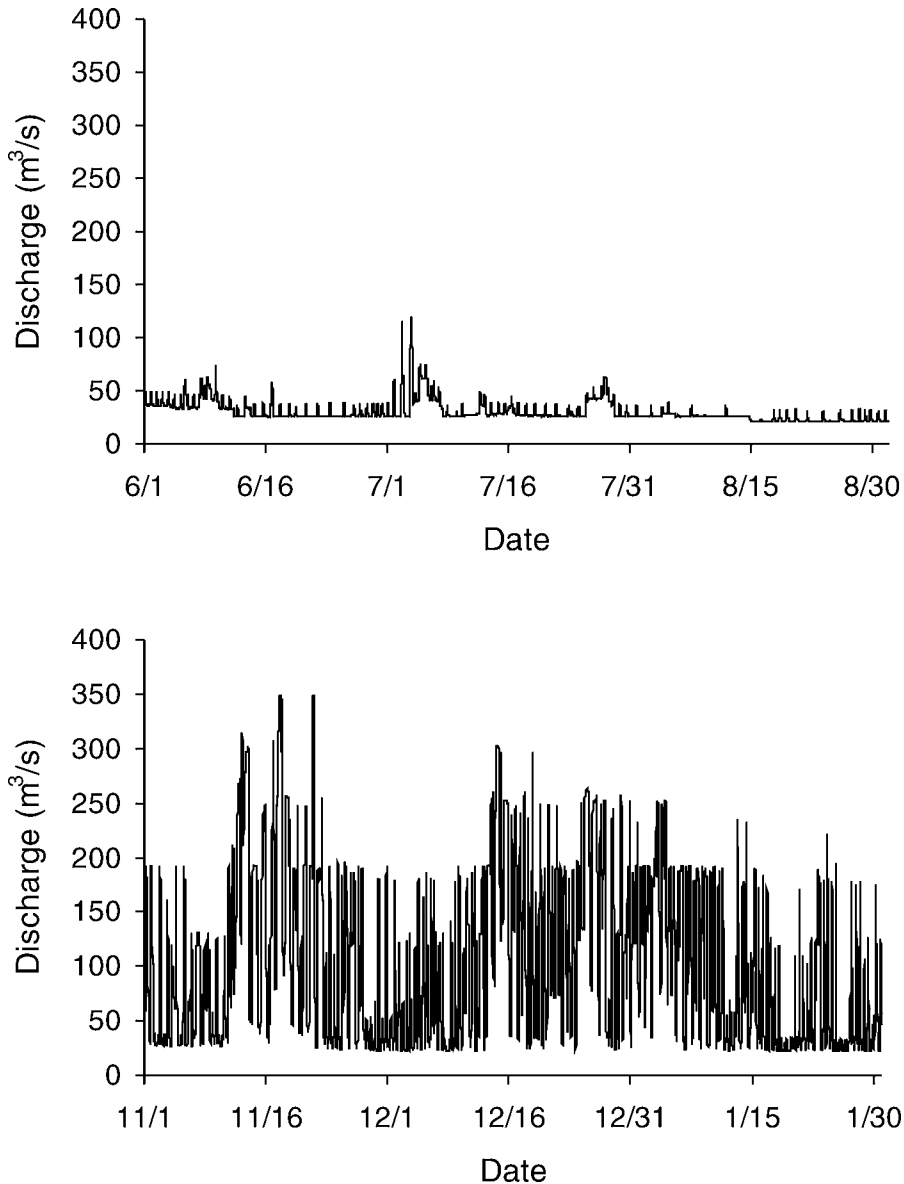


FIGURE 3.—Comparison of real-time river discharge measurements for the New River, Virginia, during run-of-river (top) and hydropeaking (below) release modes of operation at Claytor Hydroelectric Dam. Plots are real-time discharges measured from 1 June to 31 August 2003 (top) and from 1 November 2002 to 31 January 2003 (bottom).

classify substrate in areas predominantly containing shallow water, such as in our study reach where nearly 70% of the reach was less than 2 m in depth.

The impetus for this research was to fill an information gap regarding muskellunge habitat selection in southeastern warmwater rivers and to better understand how muskellunge habitat use and selection may be affected by changes in river discharge. To this end, we identified water depth as the primary habitat

variable for which muskellunge selected. Additionally, we found that river discharge significantly affected both habitat use and selection of fish. This has potentially important implications regarding the management of water release from upstream impoundments (Scruton et al. 2005). Hydropeaking can be an attractive mode of operation for power companies because it permits electricity generation during peak demand (Scruton et al. 2005). However, hydropeaking

can have drastic effects on both downstream habitat and aquatic biota (Cushman 1985; Moog 1993; Newcomb et al. 2002; Krause et al. 2005). For muskellunge as well as for other species located downstream from Claytor Hydroelectric Dam, the frequent fluctuations in discharge resulting from hydropeaking could result in significant energetic strains during portions of the year when fish are most susceptible to energetic depletion, and ultimately may lead to increased mortality for fish stocks (Scruton et al. 2005). Such indirect effects on fish stocks may be just as important as direct effects when evaluating biological implications of modes of operation for upstream hydroelectric impoundments.

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