

Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac river system

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Abstract – The northern snakehead (*Channa argus*) is a large piscivorous fish that is invasive in eastern Europe and has recently been introduced in North America. We examined the seasonal habitat selection at meso- and microhabitat scales using radio-telemetry to increase understanding of the ecology of this species, which will help to inform management decisions. After the spawning season (postspawn season, September–November), northern snakeheads preferred offshore Eurasian water-milfoil (*Myriophyllum spicatum*) beds with shallow water (~115 cm) and soft substrate. In the winter (November–April), these fish moved to deeper water (~135 cm) with warmer temperatures, but habitat selection was weak at both scales. Northern snakeheads returned to shallower water (~95 cm) in the prespawn season (April–June) and used milfoil and other cover. Habitat selection was the strongest at both meso- and microhabitat scales during the spawning season (June–September), when fish preferred macrophytes and cover in shallow water (~88 cm). Our results help to identify habitats at the risk of invasion by northern snakeheads. We suggest that control efforts and future research focus on shallow waters, and take into consideration the seasonal habitat preferences.

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Introduction

The northern snakehead (*Channa argus*) is a large, freshwater, piscivorous fish that was introduced to North America from Asia. Several populations of the northern snakehead have become established in the USA, including the Potomac River where the species was introduced as early as 1998 (Odenkirk & Owens 2005). The first established population of the northern snakehead to be discovered was found in Crofton Pond, Maryland, in 2002 and has been eradicated. Since 2002, established populations have been discovered in Virginia, Maryland, Pennsylvania, New York and Arkansas (Fuller & Benson 2009). The northern snakehead is the only snakehead species predicted to survive in temperate regions of North America (Herborg et al. 2007); however, the bullseye snakehead (*Channa marulius*) has become established in Florida and the blotched snakehead (*Channa*

maculata) has become established in Hawaii. The giant snakehead (*Channa micropeltes*) has been introduced numerous times from Tennessee northward, but reproducing populations have not become established (Fuller & Benson 2009).

The northern snakehead is considered a threat to the native fauna in temperate regions because of its broad tolerance of environmental conditions and varied diet, along with its previous success as an invader in Eastern Europe (Courtenay & Williams 2004; Herborg et al. 2007). This species thrives in shallow, vegetated waters of diverse freshwater ecosystems, including lakes, rivers, streams, reservoirs, canals and ponds (Courtenay & Williams 2004); however, knowledge of the habitat preference of the northern snakehead is limited because there have been few scientific investigations of its habitat.

Understanding the habitat preference of the northern snakehead may improve our ability to predict its

environmental impacts and to develop management strategies for this invasive species. Knowledge of the ecology of invasive species allows improvement of the quality of risk assessments by reducing biological uncertainty (Mendoza-Alfaro et al. 2009). Habitat availability is a key determinant of an invader's abundance, growth and reproductive potential. Information on habitat use may aid in estimating the likelihood of establishment of the northern snakehead in new ecosystems, and in predicting its spread and impact in systems where it does become established. Habitat preferences can also be used to infer relationships with native species; predation and competition can be expected to be highest for native species that use similar habitats. Predation by nonindigenous fishes can result in extirpation of native species (He & Kitchell 1990; Findlay et al. 2000). Similarly, competition with nonindigenous fishes can extirpate or reduce the population size of native species (Larson & Moore 1985; Blanchet et al. 2007).

Evaluation of potential impacts can inform decisions about whether to control or to eradicate invasive species. The National Park Service began controlling populations of introduced lake trout (*Salvelinus namaycush*) because severe declines in populations of native Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) were predicted, along with associated economic losses (Johnson et al. 2009). When efforts are made to control or eradicate populations of the northern snakehead, knowledge of its habitat preference can improve success rates by informing managers of habitats to target. Control of populations of the sea lamprey (*Petromyzon marinus*) in the Great Lakes was facilitated by knowledge of their spawning habitat (Smith & Tibbles 1980). In addition, future research on the northern snakehead may also benefit from baseline information on habitat use provided in this study.

Descriptions of habitat use are scale-dependent. Macrohabitat preferences of the northern snakehead are relatively well understood; it prefers shallow, muddy, vegetated habitats (Courtenay & Williams 2004) and avoids deep, flowing waters (Owens et al. 2008). Thus, our investigation focused on habitat selection at meso- and microhabitat scales. Mesohabitats are commonly described qualitatively in telemetry studies as open water, macrophytes, woody debris and similar structures (Jones & Stuart 2007). Microhabitat is more commonly described by quantitatively measuring variables such as water depth and temperature at a specific location (e.g., Daugherty & Sutton 2005).

Odenkirk & Owens (2005) reported the collection of northern snakeheads in the Potomac River from waters <2 m deep with submergent or emergent vegetation and near shorelines, channel edges or boat slips. In a radio-telemetry study of northern snakeheads in the Potomac River, Owens et al. (2008)

demonstrated preference for hydrilla (*Hydrilla verticillata*) and floating docks during the spawning season, and for hydrilla and Eurasian water-milfoil (*Myriophyllum spicatum*) after the spawning season. Their results were confounded because all of these habitats were common in their study area, and their study design did not account for habitat availability. We found no detailed studies of the microhabitat preference of the northern snakehead.

We used radio-telemetry to study meso- and microhabitat use of northern snakeheads in the Potomac River catchment. Telemetry is a popular tool for determining the habitat use of fishes, including the northern pike (*Esox lucius*), flathead catfish (*Pylodictis olivaris*), Asian carps and common carp (*Cyprinus carpio*) (Daugherty & Sutton 2005; Stuart & Jones 2006; Degrandchamp et al. 2008; Kobler et al. 2008). Additionally, we examined how habitat use changed with season. Habitat preferences of northern snakeheads are affected by seasonal changes in habitat availability such as the growth and senescence of aquatic macrophytes and changes in water temperature. Activities of northern snakeheads can be grouped into four distinct behavioural seasons (prespawn, spawning, postspawn and winter), during which different behaviours such as foraging, spawning and resting generally require unique habitats (Owens et al. 2008; N. Lapointe, pers. obs.).

Our objectives were to investigate: (i) seasonal changes in microhabitat use, (ii) microhabitat variables for predicting the occurrence of northern snakeheads each season, (iii) strength of microhabitat selection by season and (iv) mesohabitat preferences by season. Additionally, we explored how tide affected microhabitat selection and whether inactive northern snakeheads rested in different habitats than those used by active fish during winter.

Study area

Our study area encompassed Gunston Cove, Dogue Creek Bay and Little Hunting Creek, which are tributaries and embayments of the Potomac River (Fig. 1). We also sampled nearby areas of the Potomac River. These areas are shallow (rarely deeper than 3 m), have extensive aquatic vegetation, show tidal influences and have salinities of 0–3 ppt. The Potomac River is located in the eastern USA and is the second-largest tributary of the Chesapeake Bay.

Materials and methods

Tag implantation

We captured 49 northern snakeheads by boat electrofishing (438–722 mm total length, SD = 79;

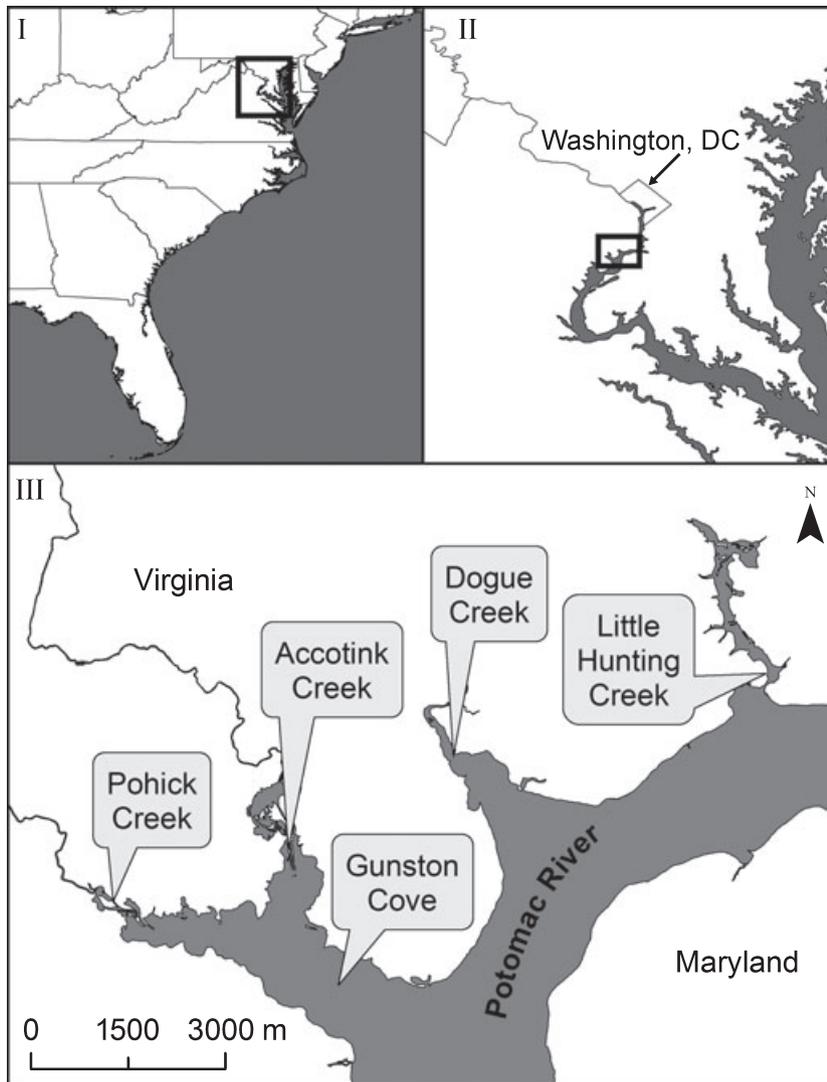


Fig. 1. Map of the study area, including creeks and embayments where habitat was measured. Resolution increases from panels I to III.

790–3489 g, SD = 795) and implanted them with radio tags in October 2006. Of these, 10 were captured and released in Gunston Cove (including Pohick and Accotink Creek embayments), 10 in Little Hunting Creek and 29 in Dogue Creek. Fish were anaesthetised with MS-222 ($200 \text{ mg} \cdot \text{l}^{-1}$), and radio-transmitters were surgically implanted into their peritoneal cavities. Incisions were sealed with single, interrupted sutures so that whip antennas trailed from the incision's posterior edge. The northern snakehead is an obligate air-breather (Courtenay & Williams 2004). Thus, the fish were observed for >15 min after surgery with their heads held above water to prevent drowning until they had fully recovered. These methods are similar to those used by Owens et al. (2008), which resulted in high tag retention and low mortality rates. All fish were captured, tagged and released 11–26 October 2006.

The radio tags (Advanced Telemetry Systems, Inc., Isanti, MN, USA) weighed 15.5 g; they had a pulse rate of 40 ppm, a pulse width of 20 ms, a warranty life

of 327 days and a battery life of 654 days. The tags transmitted at 150–151.999 MHz and were equipped with a mortality sensor that signalled when the tag did not move for >8 h. The tags weighed <2% of the mass of the smallest fish (Winter 1996). Fish were located using a four-element Yagi antenna and a Challenger scanning (Advanced Telemetry Systems, Inc., Isanti, MN, USA) receiver.

Data collection

We began tracking fish on 19 October 2006 and located fish monthly through March 2007. From April to mid-June 2007, we located fish once per week, and from mid-June to mid-August 2007, we located fish twice per week. Most tracking occurred between 06:30 and 18:30 h. We recorded UTM (Universal Transverse Mercator) coordinates of each fish's location with a Garmin (GPS 12XL) (Garmin International, Inc., Olathe, KS, USA) global positioning satellite (GPS) unit, along with date and time. Average accuracy of

locations (8.9 m; SD = 5.1) was estimated by repeatedly locating ($N = 22$) fish displaying mortality signals in open water. This was similar to the average GPS error (8.7 m; SD = 7.7), determined by marking locations ($N = 9$) at the same point on shore. Thus, locating errors appeared to be attributable to GPS error, and we were confident that fish were tracked to within 1 m of their true location (plus GPS error). Certain fish could not be reached at times because of shallow water or restricted access (e.g., military base). Habitat data were not collected on these occasions.

Detailed microhabitat measurements were made for each fish's location (deemed 'snakehead observations'). We measured water temperature (°C) and salinity (ppt) at ~10 cm below the surface with an YSI 85 metre (YSI Inc., Yellow Springs, OH, USA). We measured water clarity with a 120-cm-long turbidity tube (Wildlife Supply Company, Buffalo, NY, USA) to the nearest centimetre; lower measurements represented higher turbidity. Water that appeared turbid but still exceeded 120 cm on the turbidity tube was recorded as 120 cm. Water appearing completely clear was recorded as 150 cm. We measured depth to the nearest 5 cm with a wooden dowel. The same dowel was used to estimate per cent composition of substrate classes by prodding the substrate in multiple places and examining fine substrates clinging to the dowel. Substrate classes were soft (silt and sand), hard (sand and hard clay) and coarse (gravel, cobble, boulder). Cover was recorded as one of four categories: none, structures (floating and wooden docks, duck blinds, pillars), floating debris (algae, decaying macrophytes, wood, garbage) and woody debris (fallen trees, sunken logs, beaver dams, overhanging terrestrial vegetation and roots). The per cent of the water column filled by macrophytes and filamentous algae was estimated visually. When the water column could not be viewed because of high turbidity or macrophyte/filamentous algae surface cover, the per cent cover of the surface was used. A general, qualitative description of mesohabitat was recorded for an approximately 2-m radius around the estimated fish location.

An additional habitat measurement was made at a paired, random location for all observations from October 2006 to March 2007 and for every second week from April to August 2007 (deemed 'random observations'). The random location was determined by selecting a random compass bearing from the habitat sample and travelling 100 m in embayments or 50 m in creeks. If a shoreline or obstacle was encountered on that bearing, the direction was adjusted and travel continued until the necessary distance was reached. These distances were selected to balance the avoidance of autocorrelation of microhabitat variables between paired samples with efficiency in the field (i.e., limiting travel time). Shorter distances

were used in creeks because habitats were less homogeneous and frequent directional adjustments for obstacles and shorelines increased the travel time.

To determine how habitat use varied with tide, tide levels were estimated from historical data at <http://www.saltwatertides.com>. The per cent tide remaining was estimated based on the time a fish was located relative to high and low tides for the current tidal cycle. Tide data for Gunston Cove and Mount Vernon were used, depending on the location of each fish. Tides were divided into four periods representing high (upper 75% of tides), outgoing (74% to 26% out), low (bottom 25% of tides) and incoming (26% to 74% in).

The following seasons were defined: postspawn (16 September–15 November), winter (16 November–19 April), prespawn (20 April–7 June) and spawn (8 June–15 September). Dates were based on previous studies (Owens et al. 2008), along with data for behaviour and condition (Lapointe, N.W.R., Odenkirk, J.S. & Angermeier, P.L. unpubl. data). The day 19 April 2007 was the last day that mortality signals were detected in association with inactivity due to cold temperature. The day 7 June 2007 was the onset of peak spawning season, based on gonado-somatic indices (A. Gascho Landis, unpubl. data). Unlike Owens et al. (2008), we included December in the winter season because northern snakeheads had moved to areas where they remained throughout winter.

Data preparation

Substrate categories and vegetation types were combined to reduce the number of variables used in analyses. Filamentous algae and the three most common macrophytes (milfoil, hydrilla and coontail, *Ceratophyllum demersum*) were treated as separate variables. Rarer macrophytes were grouped into categories, based on similarities in physical shape and habitats occupied. Spatterdock (*Nuphar polysepala*) and common arrowhead (*Sagittaria latifolia*) were combined as one variable because both were found on shallow tidal flats. Bulrush (*Scirpus* spp.) and other emergent vegetation found along shorelines and shallower tidal flats were also combined into a single variable. Finally, native submergent macrophytes including chara (*Chara* spp.), water stargrass (*Heteranthera dubia*), water celery (*Vallisneria spiralis*) and water nymph (*Najas* spp.) were often found together and were combined into one variable.

Mesohabitat was classified into eight categories: (i) hydrilla beds (large areas where hydrilla was the dominant macrophyte), (ii) milfoil beds, (iii) mixed macrophyte beds, (iv) spatterdock and arrowhead beds (very shallow, often tidal, with spatterdock and arrowhead dominant), (v) open water (offshore, often turbid, with few or no macrophytes present), (vi) creek

channels (similar to open water, but with some current), (vii) inshore areas (a mix of the above categories but adjacent to shore) and (viii) wooden docks and marinas (any areas where man-made structures dominated).

Less than five per cent of the observations contained missing values because of data entry omissions or equipment failure. When possible, missing values were estimated from similar samples (e.g., missing water temperature filled in from the following observation). Observations containing missing values that could not be reliably estimated (<5%) were deleted prior to analysis.

Statistical methods

We analysed the changes in microhabitat variables for snakehead observations over time. Data for snakehead observations (i.e., excluding random observations) were graphed to show seasonal changes as scatterplots by Julian date, with trends shown as cubic splines with

the number of knots chosen *ad hoc* (Ott & Longnecker 2001). Statistical tests were also performed to estimate the significance of seasonal differences in microhabitat variables that were not likely to change over time (e.g., depth, other cover, substrate). Tests were chosen to be nonparametric (Kruskal–Wallis as omnibus, Mann–Whitney *U* as *post hoc*), with the null hypothesis that microhabitat variables for snakehead observations would be similar among seasons. All tests were conducted at 0.10 significance within the R statistical environment (R Development Core Team 2009).

We identified which variables were most useful in predicting the occurrence of northern snakeheads in each season. Logistic regression was used to estimate the snakehead microhabitat selection by season, with microhabitat variables used to distinguish between snakehead and random observations (which were interpreted as case–control samples *sensu* Keating & Cherry 2004). Microhabitat selection was evaluated separately for each season due to major seasonal differences observed in the field (Fig. 2) and shown by

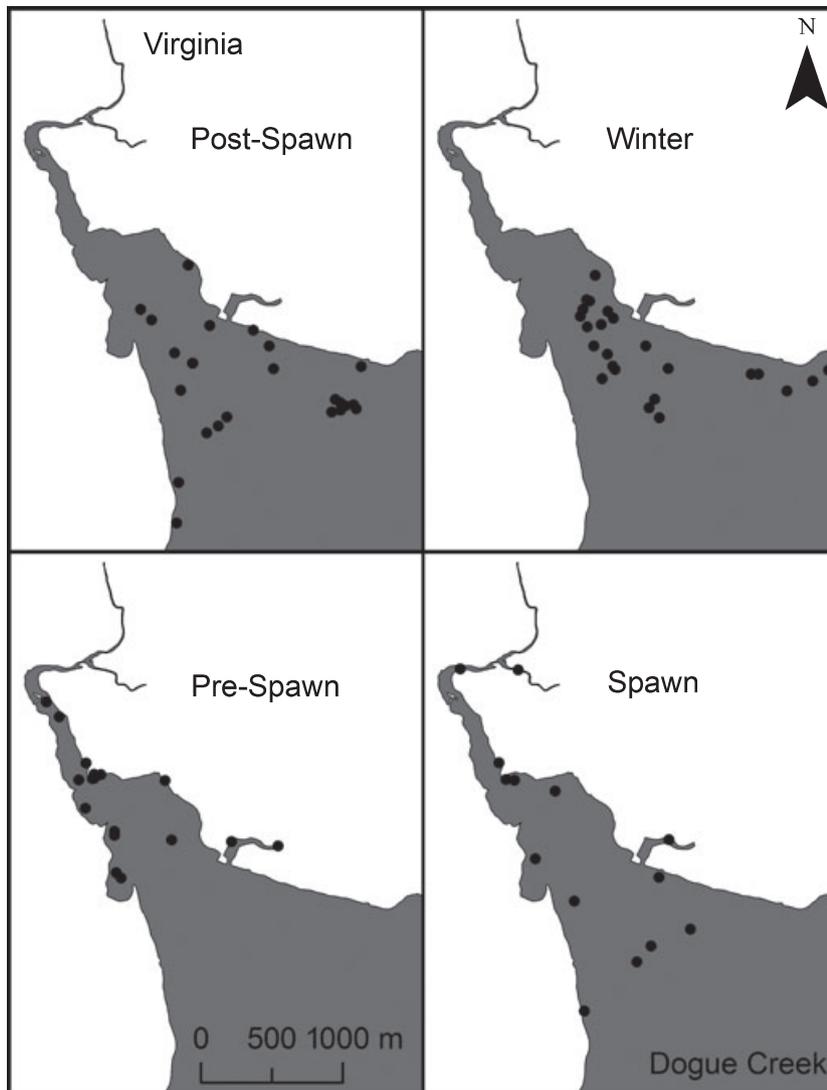


Fig. 2. Examples of northern snakehead locations (●) by season in Dogue Creek bay. Each panel shows all locations from a single tracking session in a season. Mortalities and dispersal reduced the number of locations in prespawn and spawning seasons. Dates of tracking sessions are: postspawn, 7–9 November 2006; winter, 5–7 March 2007; prespawn, 11 May 2007; and spawn, 6–12 July 2007.

results from analyses of microhabitat variables. Significant variables were identified by backwards stepwise model selection, starting with the full model (i.e., including all available variables; Ott & Longnecker 2001). Variables were dropped in reverse order of significance as estimated using Wald tests (e.g., $\hat{\theta}/se(\hat{\theta})$ compared with a normal distribution; Davidson & MacKinnon 2004). We used a 0.10 significance cut-off in the 'Design' package in R (Harrell 2008). Microhabitat selection logistic regressions did not control for tide (because this would require several additional degrees of freedom), so we performed an *a posteriori* test of the assumption that tide did not strongly influence habitat selection. To test the influence of tide on habitat selection, we performed a logistic regression distinguishing between spawning-season high and low tides (which were hypothesised to display the strongest difference due to tide). Additionally, we observed individual northern snakeheads occasionally going inactive for extended periods of time (i.e., displayed mortality signals but later were confirmed alive) during winter. To investigate whether fish selected specific microhabitats in which to remain inactive, we performed a logistic regression between active and inactive snakehead observations in winter.

We used logistic regression to identify important variables (as opposed to, say, Mann–Whitney *U*-tests) because (i) it allows the impact of individual variables to be evaluated while controlling for the effect of other important variables, (ii) it does not require specification of a sequential testing correction and (iii) it does not have distributional assumptions for independent variables (which often were proportion measures and, hence, nonparametric) or model residuals (Bewick et al. 2005). Although principal components regression and stepwise selection using the Akaike information criterion may have improved the overall predictive accuracy (Burnham & Anderson 2002), the study's focus was on the importance of individual variables, which motivated the use of untransformed independent variables.

We estimated the strength of microhabitat selection in each season using an *ad hoc* procedure developed to control for the impact of sample size (which differed among seasons) on the number of variables selected. This procedure used a nonparametric bootstrap (Efron & Gong 1983) to select a subsample of standardised size ($n = 100$) from each season, which was fit with a logistic model using all available variables. The Nagelkerke R^2 was calculated for each bootstrap iteration, and the median R^2 was used to describe strength of microhabitat selection for that season.

We evaluated mesohabitat selection for each season by comparing the distributions of mesohabitat measurements for snakeheads and random observations. We tested for each season separately using a Pearson chi-

squared test for homogeneity (significance = 0.10). Chi-squared tests were performed with JMP 7.0.1 (SAS 2007).

Results

We located fish 860 times during the study and collected an additional 528 additional random samples. Eleven fish died during the study period, and an additional 12 fish dispersed from the study area during the prespawn period. Thus, 48 fish were located 116 (+85 random) times during the postspawn period, 44 fish were located 206 (+174 random) times during the winter period, 42 fish were located 226 (+126 random) times during the prespawn period and 29 fish were located 312 (+143 random) times during the spawning period.

Overall, northern snakeheads preferred shallow (<2 m) habitats with cover; however, fish occupied distinctive parts of the study area in each season (Fig. 2). These differences were more apparent in embayments (Dogue Creek and Gunston Cove) than in Little Hunting Creek. Fish were found both inshore and offshore in outer bays during the postspawn season but moved entirely offshore into deeper water in winter. Fish stayed in the macrophyte beds that remained in deeper offshore waters until spring. During the prespawn season, fish moved upstream into inner bays, creek mouths and upstream sites in the creeks. Many fish remained in these areas during the spawning season, whereas others moved farther upstream in creeks or back to outer bays and shorelines.

Microhabitat selection was weak during the postspawn season (Nagelkerke $R^2 = 0.26$). Northern snakeheads were found primarily offshore in large milfoil beds, which were most prevalent during this season. During the postspawn season, northern snakeheads selected deeper water than during any season but winter and were less likely to be associated with other forms of cover than during the prespawn and postspawn season. Fish preferred soft substrates in the prespawn and postspawn seasons when compared with winter, but avoided coarse substrates in the winter when compared with the spawning season (Table 1, Fig. 3). At the microhabitat scale, northern snakeheads were positively associated with milfoil (habitat mean = 22%, random mean = 17%), which was the only variable selected by stepwise logistic regression (Table 2). Mesohabitat selection was nearly statistically significant, with fish most strongly avoiding open water and preferring hydrilla beds (Table 3).

Microhabitat selection was the weakest during winter (Nagelkerke $R^2 = 0.17$). During the winter, however, northern snakeheads selected deeper water with more soft substrate than during any other season and avoided other forms of cover and coarse substrate

Table 1. Seasonal means in 'Habitat' measurements.

Variable	Postspawn	Winter	Prespawn	Spawning
Depth (cm)	116 B	136 A	94 C	88 C
Other cover (%)	7 B	3 C	17 A	20 A
Soft substrate (%)	85 C	96 A	87 B	72 C
Coarse substrate (%)	1 B	1 B	3 B	6 A

Results of *post hoc* tests following Kruskal–Wallis tests (all significant at $P < 0.001$) for seasonal differences in microhabitat values are shown by letters below means. Different letters signify significant differences ($P < 0.10$) among seasons.

(Table 1, Fig. 3). Only temperature was selected at the microhabitat scale; fish preferred warmer water temperature (habitat mean = 7.5 °C, random mean = 6.9 °C; Table 2). Similarly, only temperature differed between microhabitats used by active (7.6 °C) and inactive (5.4 °C) fish (Table 2). Mesohabitat selection was not significant (Table 3).

Microhabitat selection increased during the pre-spawn season (Nagelkerke $R^2 = 0.30$). Fish moved to shallower waters with more cover than postspawn and winter seasons, and preferred soft substrate compared with the spawning season but not compared with winter (Table 1, Fig. 3). At the microhabitat scale, fish selected habitats with shallower water (habitat mean = 94 cm, random mean = 116 cm) and with more milfoil (habitat mean = 3.2%, random mean = 1.5%) and other forms of cover (habitat mean = 17%, random mean = 5%; Table 2). Mesohabitat selection was not significant (Table 3).

Habitat selection was strongest during the spawning season (Nagelkerke $R^2 = 0.49$). Fish were more likely to use coarse substrate and less likely to use soft substrate than in other seasons, but they remained in shallow waters and continued to use other forms of cover as in the prespawn season (Table 1, Fig. 3). Microhabitats were most strongly selected in the spawning season, with nine variables selected by stepwise logistic regression (Table 2). Fish selected shallower water (habitat mean = 88 cm, random mean = 118 cm) with lower water clarity (habitat mean = 108 cm, random mean = 98 cm) and with more coarse substrate (habitat mean = 5.8%, random mean = 2.4%) and other forms of cover (habitat mean = 20%, random mean = 10%). All macrophytes were preferred (milfoil habitat mean = 7.5%, random mean = 4.4%; hydrilla habitat mean = 24%, random mean = 15%; coontail habitat mean = 3.6%, random mean = 1.6%; other native submergent macrophytes habitat mean = 8.5%, random mean = 3.5%; spatterdock and arrowhead habitat

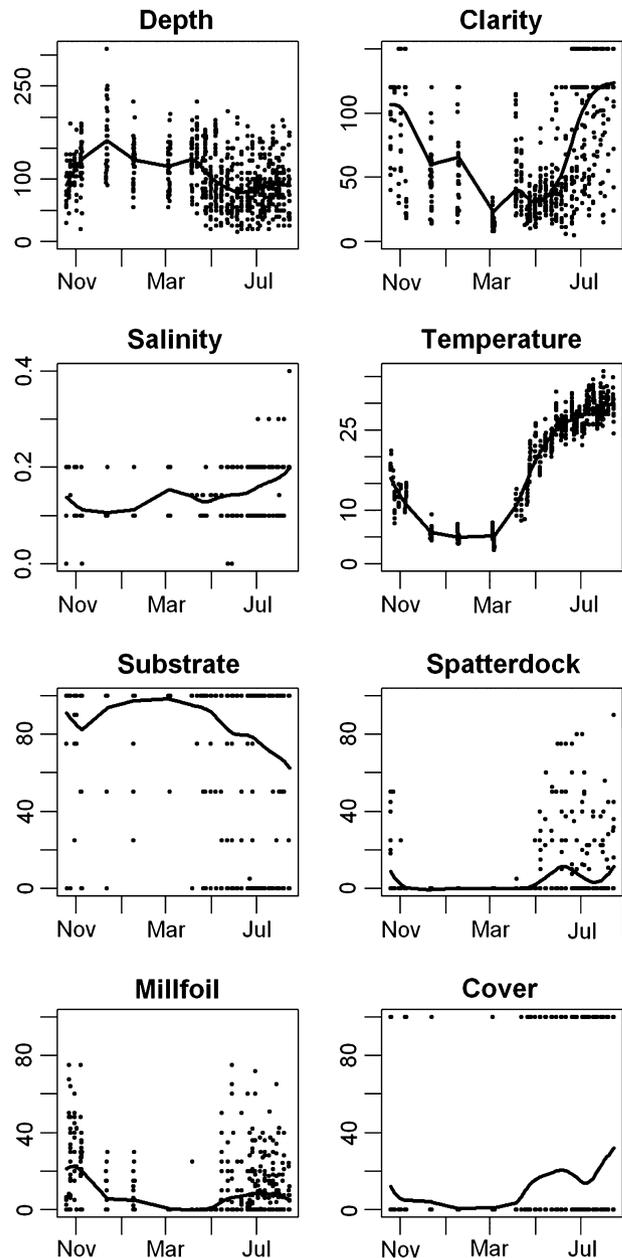


Fig. 3. Microhabitat values (Clarity = water clarity; Substrate = soft substrate, i.e., sand and silt; Spatterdock = spatterdock and arrowhead) by date. Each sample is represented by a ●, while trend over time (e.g., a cubic spline) is shown by a line. Date is shown on the X-axis. Units for the Y-axis are cm (depth, water clarity), parts per thousand (salinity), degrees Celsius (temperature) and percentage (all other variables). Variables not shown here had similar patterns; hydrilla was similar to milfoil, all other vegetation variables were similar to spatterdock and arrowhead, and hard and coarse substrate had patterns opposite to that shown for soft substrate.

mean = 5.3%, random mean = 0.9%), except bulrush and other emergent vegetation. Tide affected microhabitat selection: fish selected deeper waters at high tide (high-tide mean = 102 cm, low tide mean = 83 cm) and preferred milfoil at low tide (high-tide mean = 3.3%, low-tide mean = 6.4%; Table 2). Mesohabitats

Table 2. Parameter estimates, standard errors (SE) and Wald *P*-values for logistic regression microhabitat variables remaining after backwards selection (excluding intercepts; negative values denote a selection for the null response): (a) models distinguishing between snakehead (null) and random observations (alternative), blocked by season; (b) a model distinguishing between active (null) and inactive (alternative) snakehead measurements in winter; and (c) a model distinguishing between high-tide (null) and low-tide (alternative) snakehead observations in the spawning season.

Variable	Estimate	SE	Wald test <i>P</i> -value
(a)			
Postspawn			
Milfoil	-0.014	0.008	0.094
Winter			
Temperature	-0.064	0.034	0.062
Prespawn			
Depth	0.009	0.003	0.001
Other cover	-1.083	0.476	0.023
Milfoil	-0.041	0.019	0.033
Spawn			
Depth	0.015	0.004	0
Water clarity	0.006	0.004	0.075
Other cover	-0.935	0.356	0.009
Milfoil	-0.064	0.015	0
Hydrilla	-0.019	0.006	0.004
Coontail	-0.052	0.02	0.008
Native submergent	-0.042	0.012	0.001
Spatterdock	-0.069	0.022	0.002
Coarse substrate	-0.018	0.008	0.034
(b)			
Temperature	-0.3	0.081	0
(c)			
Depth	-0.035	0.009	<0.001
Milfoil	0.069	0.029	0.019

were most strongly selected during the spawning season. Creek channels and open water were most strongly avoided; and mixed macrophyte beds, inshore areas, and spatterdock and arrowhead beds were most strongly preferred (Table 3).

Discussion

Northern snakeheads selected unique habitats in each behavioural season, with habitat selection strongest during the spawning season at both meso- and microhabitat scales (Fig. 4). Habitat selection was most clearly demonstrated at the microhabitat scale. Overall, snakehead habitat preferences appear to be driven by an affinity for cover, including macrophytes and soft substrate. Cover types that were available and those that were preferred differed with season.

Postspawn season

During the postspawn season, northern snakehead habitat use was driven by the presence of dense beds of macrophytes (particularly milfoil and hydrilla) found offshore in shallow embayments. We conclude

Table 3. Chi-squared tests of homogeneity of mesohabitat for snakehead and random observations, blocked by four study seasons: (a) test results, with the total number of observations (*N*), and degrees of freedom (d.f.) differ among seasons because not all mesohabitat categories were observed in each season; (b) the proportion of snakehead observations in each mesohabitat category minus the proportion of random observations in each mesohabitat category.

(a)				
Season	<i>N</i>	d.f.	Pearson chi-squared	<i>P</i>
Postspawn	200	7	12.0	0.1005*
Winter	378	5	4.8	0.4378*
Prespawn	349	5	7.1	0.2136
Spawn	446	7	52.7	<0.001
(b)				
Mesohabitat	Postspawn	Winter	Prespawn	Spawn
Hydrilla beds	0.08	0.01	0.00	-0.03
Milfoil beds	0.02	0.01	0.03	0.04
Mixed macrophyte beds	0.03	0.00	0.00	0.11
Spatterdock and arrowhead beds	0.02	0.00	0.03	0.07
Open water	-0.16	-0.03	-0.06	-0.14
Creek channels	0.01	0.02	-0.06	-0.16
Shorelines	-0.01	0.01	0.05	0.09
Wooden docks and marinas	0.01	-0.01	0.01	0.02

Negative values represent a higher proportion of random observations for that category.
 *20% of cells had expected count <5, chi-squared test suspect.

that northern snakehead preference for milfoil affected microhabitat selection relative to other seasons because offshore milfoil and hydrilla beds generally had deeper water with more soft substrates than other parts of the study area.

In contrast with the prespawn and spawning seasons, we did not observe northern snakeheads in floating and woody debris along shorelines or in spatterdock and arrowhead beds, which continued to dominate shallow tidal flats. Possible explanations include an overall preference for offshore macrophyte beds as cover and habitat selection based on postspawn foraging behaviour. Northern snakeheads may prefer expansive milfoil and hydrilla beds, but such beds were not fully developed until the postspawn season. Alternate forms of cover (e.g., floating debris, spatterdock) may have been selected until macrophyte beds were more available. Additionally, foraging behaviour may have driven the selection of macrophytes beds. Northern snakeheads feed most actively during the prespawn and postspawn seasons (Gascho Landis, A.M., Lapointe, N.W.R., Angermeier, P.L., unpubl. data), and macrophyte beds may offer optimal foraging conditions during the postspawn season. Young-of-year of many prey fishes were readily available during this season and probably preferred this habitat (Grenouillet et al. 2001; Lapointe et al. 2007).

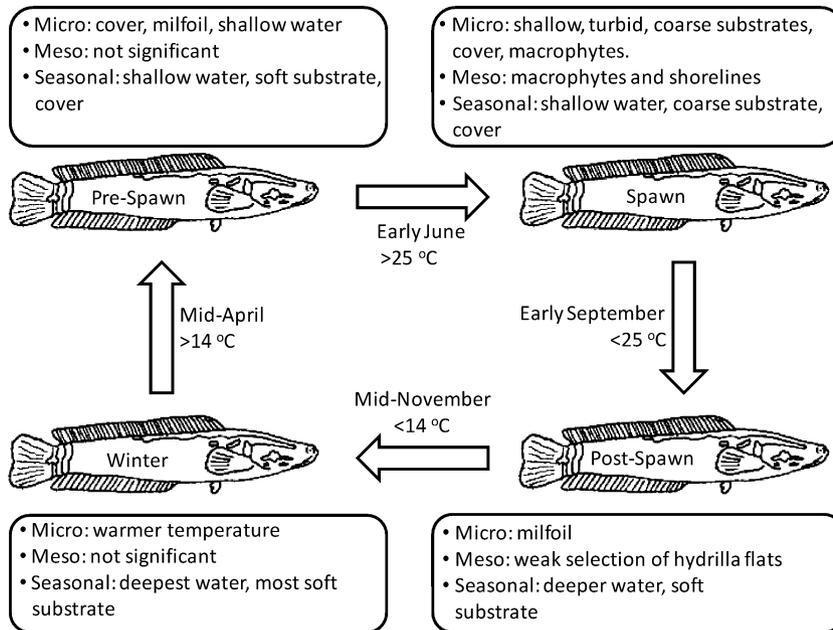


Fig. 4. Conceptual model of northern snakehead habitat use by season. Transition periods between seasons are shown by arrows, along with approximate dates and temperatures at which habitat preferences change. Text in boxes describes seasonal habitat preferences at micro- and mesohabitat scales.

Winter season

Habitat selection was the weakest during winter at both scales. Fish moved to the deepest parts of embayments where soft substrates dominated and where microhabitats were mostly homogenous. Fish may have avoided shallow, inshore areas despite the cover available there (docks, woody debris, etc.), because these areas exhibited larger temperature fluctuations. Our results showed that active fish selected warmer habitats, possibly explaining the consistent large (>500 m) movements observed during winter (N. Lapointe, pers. obs.). Conversely, remaining in cooler waters may have driven northern snakeheads into a state of torpor, where movement ceased for >8 h.

Despite the nonsignificant associations between fish and macrophytes or other forms of cover in winter, northern snakeheads may still have selected habitats based on cover. Soft substrate may offer a form of cover, given observations of northern snakeheads burrowing in sediments when water was removed from ponds (Courtenay & Williams 2004). We observed this behaviour in shallow, open water when releasing fish after tag implantation. Additionally, our habitat observations were limited by higher turbidity during the winter months. We observed sparse milfoil throughout the winter, and we often found it on the boat anchor even when it was not observed from the surface. Northern snakeheads may have selected deeper offshore habitats for cover provided by sparse milfoil in winter.

Prespawn season

During the prespawn season, fish moved back to shallower waters of inner bays, creek channels and

embayment shorelines, which often offered cover in various forms. We attribute associations with milfoil to a preference for the only overwintering macrophyte beds. Macrophyte growth had begun, but macrophytes remained rare until the end of the prespawn season. Sparse patches of overwintering milfoil may have provided cover during the early prespawn season. Preference for macrophytes may have been driven by feeding behaviour. Feeding rates increased during the prespawn season (Gascho Landis et al., unpubl. data), and prey were probably concentrated along shoreline cover and in macrophyte beds (Werner et al. 1983). Additionally, shallow habitats may have been warmer and more hospitable than in winter, allowing fish to move to inshore areas with abundant cover.

Spawning season

Habitat selection was the strongest during the spawning season at both spatial scales. Coarse substrates were most commonly selected during this season and were found primarily along shorelines, which northern snakeheads may have been using for spawning. Northern snakeheads construct and guard nests in patches of macrophytes (Courtenay & Williams 2004), and nests must be constructed in areas that protect floating eggs from current and wave action (Gascho Landis & Lapointe 2010). Fish moving to protected inshore areas for spawning purposes were thus associated with coarse substrates. Northern snakeheads also preferred macrophytes during the spawning season, likely for spawning and cover. We could not determine why northern snakeheads preferred lower water clarity, given that clarity increased in patches of macrophytes where sediment could settle from the

water column. Strong mesohabitat preferences may have reflected a preference for cover and selection of spawning habitat; open water and creek channels were most strongly avoided during this season.

Other observations

Our observations of northern snakehead habitat selection with respect to tides did not match our analytical results. At high tides, we frequently observed northern snakeheads in spatterdock/arrowhead beds and patches of dense emergent vegetation in very shallow (<30 cm) water. As the tide receded, northern snakeheads moved to the margins of these habitats, presumably holding to cover and feeding on prey being pushed out by the tide. The proportion of individuals exhibiting such behaviour was low, explaining the lack of statistical evidence for this pattern. Instead, milfoil was shown to be important at low tides, when other cover was probably unavailable. Overall, our observations and results suggest that tide played a relatively minor role in habitat selection and that differences among tides did not have a major impact on other microhabitat associations.

We rarely observed northern snakeheads while tracking. If we remained still near tagged fish for more than 15 min, we frequently observed them swimming. This suggests that northern snakeheads do not always remain in cover, as opposed to ambush predators such as Esocids, which often remain stationary for extended periods (Webb & Skadsen 1980). Northern snakeheads appeared to exhibit a fleeing response to nearby cover in response to tracking activities but did not appear to travel far (i.e., fish rarely seemed to be 'pushed' a significant distance by the boat). Although we expect that microhabitat data were somewhat biased towards the presence of cover (debris, macrophytes, soft substrate), we believe that nearby availability of such cover is integral to northern snakehead meso- and microhabitat selection.

Study design

Our results suggest that the evaluation of habitat selection is most informative at the microhabitat scale. We often observed differences in habitat selection at the microhabitat scale when mesohabitat selection did not occur. Telemetry studies of fishes often focus on the mesohabitat scale. Habitat is categorised, and preference is described by identifying the most common habitats observed (e.g., Jones & Stuart 2007; Owens et al. 2008) or comparing use and availability (e.g., Degrandchamp et al. 2008). Fewer telemetry studies have measured microhabitat variables (but see Degrandchamp et al. 2008; Okland

et al. 2005), although habitat availability (e.g., measuring microhabitat at random sites) is rarely considered. Contrary to Owens et al. (2008), we did not find strong selection of hydrilla and wooden docks during the spawning season, after accounting for habitat availability. Other studies have mapped habitat using remotely sensed data or field samples (e.g., Paukert & Willis 2002; Daugherty & Sutton 2005; Kobler et al. 2008); however, seasonal changes in habitat conditions coupled with low within-season sample size prevented us from reliably mapping habitat in the study area. Although spatial autocorrelation of snakehead and random observations may have inhibited the detection of mesohabitat selection during some seasons (e.g., postspawn, when fish were found in relatively homogeneous offshore macrophyte beds), this was not always the case. During the prespawn season, mesohabitat selection was not detected, even though unique mesohabitats were regularly found within 50–100 m of snakehead observations.

We believe our results are typical for the Potomac River catchment, even though annual differences in rainfall and temperature may affect the habitat availability and selection by northern snakeheads. We expect that only minimal errors in logistic regression estimates of microhabitat selection (either spurious identification of variables or inaccurate estimation of parameters) may have arisen from variables for which we did not control, such as individual ID or tide. Failure to compensate for individual ID (i.e., as a fixed effect) may cause biases when the number of individuals is small (Otis & White 1999); however, our study located 29–48 individuals in each season.

We did not measure habitat use during late spawning season or early postspawn season, from mid-August to mid-October. The time when northern snakehead transition from specific microhabitats selected during the spawning season to homogenous macrophyte beds selected during the postspawn season remains unknown, although we expect this transition to be somewhat gradual. During the early postspawn period, water temperatures averaged around 20 °C and hydrilla was probably dominant over milfoil; however, we expect that general habitat preferences were similar to those observed in late postspawn season (i.e., offshore macrophyte beds).

Management insight

The information provided here can be used to further refine risk assessments, infer potential impacts and identify potential northern snakehead habitats in other systems. The invasibility of an ecosystem can be estimated by the availability of important habitat characteristics such as soft substrates, macrophytes and other forms of cover. Potential impacts can be

estimated by inferring predation through habitat overlap with prey species, and competition through habitat overlap with other piscivores. For example, we commonly observed prey such as *Lepomis* spp. and *Fundulus* spp., and piscivores such as largemouth bass (*Micropterus salmoides*) in similar habitats as northern snakehead (N. Lapointe, pers. obs.). In the Mississippi and Hudson river drainages where northern snakehead have recently established (Fuller & Benson 2009), our results can help managers identify likely habitats and locate fish.

Our results complement earlier suggestions that control may be most effective during the spawning season prior to juvenile dispersal (Jiao et al. 2009) when northern snakeheads are least mobile (N. Lapointe, pers. obs.), and can be used to develop and refine control strategies for northern snakehead. We have provided detailed information on habitat use of northern snakeheads in each behavioural season, allowing collection efforts to be focused on locations where fish are most likely to be found. Additionally, our results show that habitat selection is the strongest during the spawning season, suggesting that locations likely to harbour northern snakehead can be most easily targeted at this time of year.

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