# Articles

# A Geospatial Approach for Estimating Suitable Habitat and Population Size of the Invasive Northern Snakehead

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# Abstract

Northern snakehead Channa argus, an invasive predatory fish species from Asia, may continue to establish itself throughout temperate areas of the eastern United States, particularly in shallow vegetated habitats of ponds and streams. The species was first collected in the Potomac River in 2004 and has become successfully established in several major rivers within the Chesapeake Bay watershed. The objectives of this work were to develop habitat suitability criteria using a novel methodology that combines geographic information systems technology and fish surveys to estimate population sizes. A combination of catch data and reported or empirically derived habitat relationships were used to analyze seasonal distributions (March-October) in two tidal freshwater tributaries of the Potomac River: Nanjemoy Creek (2013) and Chopawamsic Creek (2010-2013). Adults were collected in relatively deeper sections of the streams (average depth 0.7–1.0 m) with a low cover of submerged aquatic vegetation (0–21% of site). Using additional distributional data, we identified suitability criteria as: 1) edges of submerged aquatic vegetation that included 5 m of vegetation and 5 m of adjacent open water; 2) less than 30% of mid-channel distance from shore, which may or may not include submerged aquatic vegetation; and 3) the upper 15% of the tidal freshwater stream. An adult population estimate derived from a suitable area in Pomonkey Creek (a tributary of the Potomac River) and estimated densities from Nanjemov Creek and Chopawamsic Creek (i.e., three adults/ha) was not different from that expected using electrofishing surveys. Assuming approximately 7,093 ha of suitable habitat and three adults/ha, the number of adults was predicted to be 21,279 for 44 major tidal freshwater tributaries of the Potomac River. This is our first estimate of population size of northern snakehead for any river of the Chesapeake Bay watershed and its accuracy will undoubtedly improve as additional studies report variation in density for other tributaries. Because of the species' ability to establish itself in temperate climates, it is important to engage the public to prevent additional releases of northern snakehead, especially to vulnerable habitats.

Keywords: Channa argus; spatial; injurious; Lacey Act; ecology; distribution; estuary

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# Introduction

Northern snakehead Channa argus, an invasive predatory fish species from Asia, occupies shallow vegetated habitats of ponds and rivers (Courtenay and Williams 2004; Lapointe et al. 2010; Figure 1). In its native range of China and other smaller countries of Asia, the species thrives in stagnant, slow-moving streams or lakes



**Figure 1.** Northern snakehead *Channa argus* (approximately 525 mm and 1.4 kg) collected on the Potomac River (Chesapeake Bay watershed) by Ryan Hagerty (U.S. Fish and Wildlife Service).

characterized with muddy habitats and aquatic vegetation (Kumar et al. 2012). Because of its wide tolerance of thermal temperatures and hardiness, it could potentially spread throughout temperate climates of eastern North America (Herborg et al. 2007; ANSTF 2014). The species was initially discovered in the Potomac River in 2004 and has an established population (Odenkirk and Owens 2005) that has naturally spread to other major drainages of the Chesapeake Bay watershed (Benson 2014). The expanding distribution of northern snakehead to drainages adjacent to the Potomac River can be attributed to its natural ability to disperse long distances (Lapointe et al. 2013). Snakeheads could pose a threat to native ecosystems (Courtenay and Williams 2004; Saylor et al. 2012) by reducing biodiversity (Sala et al. 2000), altering food webs (Vitule et al. 2009), spreading pathogens (Hill 2011; Iwanowicz et al. 2013), and ultimately threatening recreational fisheries (Crooks 2005; Love and Newhard 2012). Monitoring and protecting ecosystems from invasive species can include an approach that identifies and quantifies suitable habitats for those species, which may in turn be used to help predict abundance or population size. Here, we develop a novel methodology to predict population size based on suitable habitat for northern snakehead (hereafter, snakehead).

Habitat use by snakeheads varies seasonally and has been studied to assess potential impacts to sympatric species (Lapointe et al. 2010). During spring, snakeheads move into upstream habitats in response to precipitation and flooding (ANSTF 2014) and enter downstream, deeper habitats during winter (Lapointe et al. 2010). The distribution of the species in Virginia tributaries of the Potomac River has indicated preference for shallow habitats (< 2 m) that are dominated by submerged aquatic vegetation (SAV; Lapointe et al. 2010) or near docks. Fish avoid open waters (Odenkirk and Owens 2005; Lapointe et al. 2010). Such microhabitat preferences provide better insight into habitat suitability than mesohabitat preferences for snakeheads (Lapointe et al. 2010).

Habitat suitability concepts have long been used to identify essential fish habitat for both sport fishes (Stuber et al. 1982; Love 2011) and rare-threatened-endangered species (Niklitschek and Secor 2005). More recently, fish ecologists have begun linking habitat suitability and population dynamics using geographic information systems (GIS) to predict species responses to habitat disturbances (Akçakaya 2001; Hart and Cadrin 2004; Wang et al. 2013). In invasive species ecology, a similar framework can be developed to determine whether a habitat is suitable for establishment (Shafland and Pestrak 1982) and to efficiently target habitats for population control, both of which could limit spread of the species into new habitats (Vander Zanden and Olden 2008). Delineating suitable habitat for snakeheads supports objectives of the current National Control and Management Plan for Members of the Snakehead Family (Channidae) by the Aquatic Nuisance Species Task Force (ANSTF 2014) by improving efficiency of population control methods, identifying potentially vulnerable habitats, and estimating population sizes. The ANSTF was established as an intergovernmental organization that implements the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990.

The objectives of this work were to: 1) analyze seasonal distributions of snakeheads in two tidal freshwater streams; 2) use results from those analyses to develop habitat suitability criteria; 3) determine if the product of suitable habitat area and densities from neighboring streams (number of adults/ha) provides a reasonable adult population estimate in a third, independent stream; and 4) estimate the adult population size of snakeheads in the Potomac River. We hypothesized that snakehead occurrences would be most probable in upstream, nearshore habitats that were shallow (< 2 m) and vegetated.

# Methods

#### Habitat

Chopawamsic Creek and Naniemov Creek are freshwater or oligohaline. The proportion of wetland shoreline is similar between Chopawamsic Creek (57%) and Nanjemoy Creek (58%). The remainder of the shoreline is forested. There is more SAV in Chopawamsic Creek (106.5 ha in 2012 or 67.3%) than in Nanjemov Creek (26.9 ha in 2012 or 28.7%). At incoming or high tides, depth in the surveyed area was similar between Chopawamsic Creek (surveyed maximum depth = 1.3 m, average depth = 0.7m, SD = 0.2) and Nanjemov Creek (surveyed maximum depth = 1.8 m, average depth = 0.7 m, SD = 0.4). Depth in both surveyed and nonsurveyed areas is fairly uniform in Chopawamsic Creek. In contrast, the maximum depth in Nanjemoy Creek at mean low water could vary between 3 and 4 m within the channel (NOAA 2007), which was not sampled.

## Sampling

Snakeheads were sampled biweekly at Nanjemoy Creek and Chopawamsic Creek beginning March 2013 until October 2013, and at least monthly (March-October) from Chopawamsic Creek between 2010 and 2012. Sampling was conducted parallel to shore and continuously with a Smith-Root electrofishing boat (direct current, 340-1,000 V, 30–120 pulses per second, 6–32 A) equipped with a generator-powered pulsator suitable for surveys in tidal freshwater (generator-powered pulsator 7.5 or 9.0). Because conductivity varied between 89 and 3,056 µS among sampling events (Table S1), electrofishing settings varied accordingly to produce power that resulted in visible electrotaxis of fishes. The path was recorded using handheld Magellan global positioning system (GPS) units. Distance from shore usually varied to within 20 m of the median path among sampling events (Figure 1). At the bow of the electrofishing boat, two netters captured snakeheads. Once the fish was captured, a GPS coordinate was recorded for the site of capture. The GPS locations had a positional error of 2-3 m for all sites, were corrected in the GIS (when necessary), and only approximated the location of the fish at the time of capture. A site of capture was defined as the latitude and longitude of the point where snakehead was removed from the water, and the coordinate was given a radius of 5 m to yield a site area of 78.5 m<sup>2</sup>. Each captured snakehead was measured for total length. However, only sexually mature adults (> 300 mm; Odenkirk et al. 2013) were tagged and used to estimate population sizes (see below). These fish were marked with orange Floy T-Bar tags and released. The tag was inserted into the dorsum and near the base of the dorsal fin. A tag number and instructions to report and kill the fish if caught were inscribed on the tag.

# Habitat attributes defined

Georeferenced sites of capture were imported to a GIS. Using ArcGIS (Version 10.2, ESRI), habitat attributes for each site were measured. These attributes included shoreline type, position in the stream, and in-stream variables. Shoreline type was measured as occurrence of snakehead within 50 m of forested shoreline or wetland shoreline; if no shoreline was within 50 m of capture, then it was considered a capture in open water.

Position in the stream included: 1) proximity of each fish to the most upstream, tidal freshwater end; and 2) proximity of each fish to the shoreline. Distance was measured from the mouth of the stream to the site of capture using the measurement ruler in ArcGIS. The distance of the capture site from the mouth of the stream was divided by the length of the stream, which was considered the proximity to upstream habitats. If a snakehead was caught at the farthest upstream site, then the proximity to upstream habitats was 1.0. In addition, distance was measured from the shoreline to the site where snakehead was captured. The distance from the shoreline was divided by half of the channel width to quantify the proximity to the mid-channel. If a snakehead was caught at the mid-channel, then the proximity to the mid-channel was 1.0. Proximities to upstream habitats and to the mid-channel were suitability indices for constructing habitat suitability criteria.

In-stream variables included depth and SAV distribution. Depth soundings were taken along the survey path for approximately every meter at incoming to high tide using Humminbird Side Scan Sonar (version 798i) or a Garmin depth finder (model 440s). Data for the 2012 SAV distribution were added to the GIS using data collected during fall by the Virginia Institute of Marine Science (2013). Within each site area (area =  $78.5 \text{ m}^2$ ), the area of SAV was calculated for each site using the measuring tools within ArcGIS. Area of SAV was divided by the area of the site to yield a percentage, which was then converted to rank variables: SAV present (rank = 1) or absent (rank = 0); and complete SAV cover (rank = 1) or not (rank = 0). Percentages were used for general descriptions, but ranks were used for the probit regression model (below) to simplify the interpretation of the results.

#### Habitat suitability criteria

We followed a general methodology outlined by Store and Jokimäki (2003) to establish habitat suitability criteria. Habitat suitability criteria were developed by synthesizing results from three analyses: an ArcGIS-based optimized hot-spot analysis, a more traditional probit regression analysis, and an odds ratio that explicitly tested whether there were seasonal differences in the odds that snakehead would be found in SAV. An optimized hot-spot analysis and probit regression analysis yielded insight into habitat suitability, but importantly differed because: 1) optimized hot-spot analysis identified patterns in distribution that were, a posteriori, independently explained with predictor variables, whereas probit regression analysis directly related patterns to predictor variables; and 2) optimized hot-spot analysis examined patterns using methodology (e.g., grid size) defined by ArcGIS with parameters selected by the researchers, whereas probit regression analysis examined patterns using methodology directly defined by the researchers.

To assess the utility of the suitability criteria, habitat variables were measured to yield suitability indices for a separate and independent target area, Pomonkey Creek. Using ArcGIS, criteria were applied to spatial layers for Chopawamsic Creek, Nanjemoy Creek, and Pomonkey Creek. For each layer, a pixel was weighted with 1 for suitable habitat and 0 for unsuitable habitat. From these weighted pixels, maps were hand drawn using ArcGIS to illustrate habitat as either suitable or not suitable. The areas of suitable habitat (hectares) for Chopawamsic Creek, Nanjemoy Creek, and Pomonkey Creek were calculated by summing the area of weighted pixels of each stream using ArcGIS.

Optimized hot-spot analysis. The optimized hot-spot analysis included all georeferenced snakehead captures. It was implemented with ArcGIS to identify statistically significant spatial clusters of capture sites at the appropriate spatial scale of analysis using nearest-neighbor distances among sites, as well as correct for multiple testing and spatial dependence with a false discovery rate correction method. The results were limited to sites sampled by the electrofishing boat and did not include all potential sampling sites within each stream. The optimized hotspot analysis calculates a Getis-Ord Gi\* statistic for each capture site. This statistic is the sum of weighted nearestneighbor distances among captures for each capture site subtracted from the average weighted distance among captures for all capture sites. It is standardized by the standard deviation of the average. This statistic is essentially a z-score for each capture site with a value that corresponds to whether it clusters with other capture sites. Capture sites with large z-scores are those with intense clustering of captures.

The optimized hot-spot analysis began analyzing distribution by creating a polygon feature class from the capture sites (i.e., points). To create this polygon, the Create Fishnet tool within ArcGIS was used to construct a polygon grid over the points using a grid size that was optimized for spatial scale (i.e., grid area was weighted with a scalar that was a function of the average and median nearest-neighbor distances among all capture locations) (Chopawamsic Creek grid area =  $156 \text{ m}^2$ ; Nanjemoy Creek grid area =  $200 \text{ m}^2$ ). The optimized hotspot analysis then performed a Spatial Join to join capture site locations with the polygon and determined the number of capture sites within each grid of the polygon. The spatial join produced a polygon feature class that excluded grids without capture locations. Significance of the z-scores within each grid was determined when the sum of z-scores for capture site locations unexpectedly exceeded that sum for all capture locations within the stream. Significance was determined for the z-score using a z-table for  $\alpha = 0.05$  and  $\alpha = 0.01$ and significant grids were termed "hot spots."

Clusters of hot spots (i.e., nonoverlapping groups of adjacent hot spots) were identified to calculate suitability indices for each season and stream. The suitability indices included proportional cover and rank of SAV, proximity to mid-channel, and proximity upstream. Each suitability index was weighted by total area of the hotspot cluster to determine the weighted average among all hot-spot clusters for each season and stream. Although not used for analysis because it varies with tide, a grand mean of average sampling depth among hot-spot clusters was also calculated for each season and stream to help describe habitats used by snakehead; all depth soundings were averaged within each hot-spot cluster.

Probit regression analysis. To complement findings from the optimized hot-spot analysis, a probit regression model was used to determine if occurrence was predicted by habitat variables. The models related presences (Chopawamsic Creek = 304; Nanjemoy Creek = 209) and absences (Chopawamsic Creek = 75; Nanjemoy Creek = 99) of snakeheads to habitat variables that included: rank cover of SAV, proximity upstream, proximity to the mid-channel, and the interaction of proximity upstream and proximity to the mid-channel. To compute these variables for areas of absence, rectangles with an area of 78.5 m<sup>2</sup> were drawn to encompass 30 m of each side of the median sampling path. Rectangles where snakeheads were captured were excluded and one rectangle capable of being surveyed was randomly selected every 1 km along the surveyed path. A probit regression model was fit to all available data, to data for each stream, and to data for each season per stream. Before modeling, autocorrelation among habitat variables was examined using pair-wise Spearman's rank correlations (r). Though r was usually statistically different from 0, most predictors had only small correlations with one another  $(-0.3 \le r \le 0.3)$ . The correlation of two predictors (presence/absence of SAV and total cover/not total cover of SAV) was slightly high (r = 0.68; 95%) confidence interval = 0.03), but this level of autocorrelation did not affect interpretation of results because models with one or the other predictor had similar results to those including both predictors. The probit regression model used a modified Gauss-Newton algorithm and maximum likelihood to determine the significance of each habitat variable that predicted occurrence of snakehead (SYSTAT version 13.0, Systat Software, Inc.). The variance in proximity to mid-channel and variance in proximity upstream were not normally distributed and were transformed by the arcsine (square root) for analysis.

Odds ratio. The odds of finding snakehead in SAV was calculated as the proportion of snakeheads within 5 m of SAV divided by the proportion of snakeheads that was not caught within 5 m of SAV. For each capture location, the measuring tool was used to determine if the location occurred within 5 m of SAV. The odds ratio was calculated for each season and each stream to determine whether the ratio differed seasonally and between streams.

## Population estimate

Snakeheads that were caught and recaptured during the course of boat electrofishing surveys were used to estimate population sizes in Chopawamsic Creek (five at least biweekly periods in 2011; one biweekly period in 2012; two biweekly periods in 2013) and Nanjemoy Creek (four biweekly periods in 2013). These periods were used to provide population estimates because many sampling events failed to yield recaptures needed to generate a population estimate. A Chapman-modified Lincoln-Peterson equation was used to estimate population size  $(N_t)$  for sexually mature snakehead. The Chapman modification of the Lincoln-Peterson estimator is the most common method of population estimation in some large rivers (Curry et al. 2009). The Chapman modification of the Lincoln–Peterson estimate of  $N_t$  was:  $N_t = ([M + 1] \times$ [C + 1])/(R + 1), whereby M is the number of marked fish during the first sampling event (minus the number of tagged fish harvested by anglers within the markrecapture period), C is the number of captured fish on the subsequent sampling event, and R is the number of recaptured, marked fish on the subsequent sampling event. Standard deviation was the square root of the estimates' variance, which was calculated as:  $([M + 1] \times$  $[C + 1] \times [M - R] \times [C - R])/([R + 1]^2 \times [R + 2])$ . Marked fish were released at the site of capture, throughout the study reach, and allowed to redistribute themselves for 7-14 d. Fish were not allowed to redistribute themselves for longer than 14 d to minimize the influence of immigration and emigration, which can bias population estimates, and reduce bias associated with seasonal differences in capture probabilities. Numerous  $N_t$  estimates were computed for each stream to reduce error in the average for each stream and measure a standard deviation for the average. To contend with the possibility of recapturing a very small proportion of the population, variance in the population estimate was bootstrapped. The average and standard deviation of  $N_t$ for each stream was used to generate a normal distribution of 10,000 values, from which a 90th percentile of  $N_t$  was determined.

The 90th percentile of  $N_t$  (or  $N_t$ -90) was used as a liberal measure of population size and in two ways. First,  $N_t$ -90 was used to estimate catch probability (q) for each sampling event by dividing catch per hour (CPH, i.e., number of snakehead caught divided by the number of hours spent electrofishing) by  $N_t$ -90 (Fischler 1965). A median q among all surveys was determined for Nanjemoy Creek and Chopawamsic Creek. An average between the median as for Nanjemov Creek and Chopawamsic Creek was calculated and used to estimate population size for Pomonkey Creek (see below). Second,  $N_t$ -90 was also used to estimate density of the species by dividing  $N_t$ -90 by the area of suitable habitat predicted for each stream (as above). The density of fish for each stream was also used in predicting population size for Pomonkey Creek.

Population size estimates for Pomonkey Creek were compared between that calculated from habitat suitability and that calculated using a CPH and q. A population size estimate using suitable habitat was relatively easy to estimate by multiplying the area of suitable habitat of Pomonkey Creek by the rounded density (adults/ha) for Nanjemoy Creek and Chopawamsic Creek. An empirically derived  $N_t$  was calculated with a CPH that was averaged among intensive field sampling events: three consecutive events (20-22 May 2014) and one sampling event on 11 June 2014. Pomonkey Creek was sampled in a similar manner as Nanjemoy Creek and Chopawamsic Creek with the full length of each shoreline of the stream sampled continuously. The CPH was divided by q averaged between Nanjemoy Creek and Chopawamsic Creek. To generate a 95% confidence interval for this empirically derived  $N_t$ , average CPH was allowed to vary log-normally using the standard deviation of the four sampling events and q was allowed to vary within 10% of its mean in a Monte Carlo simulation (N = 10,000iterations). Monte Carlo simulation was performed using Microsoft Excel (version 2003). Statistical difference between  $N_t$  derived from CPH and  $q_t$  and  $N_t$  estimated from suitable habitat was assumed if the latter was not included within the former's 95% confidence interval.

We extrapolated our results to estimate population size within 44 tidal freshwater streams of the Potomac River. The total area of suitable habitat was computed for the Potomac River (as above). The majority of the main stem of the Potomac River (except the most upstream reaches of the Potomac River; Figure S1, Supplemental Material) was excluded from the habitat suitability estimate because the main stem may only be used to migrate during spring (Lapointe et al. 2013). However, in some areas of the main stem, there are shallow areas with macrophytes that are utilized by snakeheads after the spawning season (pers. comm., N. Lapointe, Nature Conservancy of Canada). These areas require further study, but were not included in this population estimate because 90% of snakeheads reported by anglers (2009-2014) were captured in tributaries (unpubl. data, J. Newhard). The area of suitable habitat for the 44 streams of the Potomac River was multiplied by the density of snakeheads to generate a population size in the Potomac River.

#### Results

#### Distribution

There were 513 unique sites where sexually mature fish were captured in Chopawamsic Creek (N = 304) and Nanjemoy Creek (N = 209; Text S1, Table S1, Supplemental Material). At 27 sites in Chopawamsic Creek and 17 sites in Nanjemoy Creek, multiple snakeheads were captured (Chopawamsic Creek: N = 78, Nanjemoy Creek: N = 22), yielding totals of 380 and 231 captured individuals, respectively. Juveniles were collected in Chopawamsic Creek (N = 87) and Nanjemoy Creek (N = 2). Each time a juvenile was collected, an adult ( $\geq 300$ mm total length) was collected as well.

Fewer snakeheads were caught in open-water habitats than near shorelines (Table 1); however, less open water was sampled than habitats near shoreline (Figure 2). Although snakeheads were not commonly caught in open water throughout the year, they were more often caught in open water during summer and fall (Table 1). There were also seasonal differences in the types of shorelines near which snakeheads were caught. Snakeheads were less commonly caught near forested shorelines during summer and fall (Table 1). **Table 1.** Descriptive seasonal habitat conditions for unique sites (*N*) where northern snakehead *Channa argus* individuals were collected in Chopawamsic Creek (Chop; 2010–2013) and Nanjemoy Creek (Najy; 2013), which are two tidal freshwater streams that are tributary to the Potomac River (Chesapeake Bay watershed). A chi-square test was used to determine if the percentage of snakeheads collected near forests (% Forested), wetlands (% Wetland), or in open water (% Open water) differed significantly from a 50–50 expectation (\* for P < 0.05; n.s. = nonsignificant; n.a. = not available); percents may not sum to 100% because fish may be near two shoreline types.

|   | Chop                     |                          |                          | Najy                     |                          |                          |  |
|---|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--|
|   | Spring                   | Summer                   | Fall                     | Spring                   | Summer                   | Fall                     |  |
| Ν   | 128                      | 92                       | 87                       | 171                      | 29                       | 9                        |  |
| Average (SD) depth (m)                          | 0.72 (0.17)              | 0.73 (0.19)              | 0.77 (0.20)              | 0.77 (0.39)              | 0.79 (0.34)              | 0.75 (0.44)              |  |
| Average (SD) proportion SAV <sup>a</sup>        | 0.29 (0.43)              | 0.42 (0.48)              | 0.39 (0.47)              | 0.08 (0.21)              | 0.04 (0.11)              | 0.16 (0.25)              |  |
| Average (SD) proximity upstream                 | 0.48 <sup>b</sup> (0.31) | 0.42 <sup>b</sup> (0.30) | 0.44 <sup>b</sup> (0.34) | 0.21 <sup>c</sup> (0.13) | 0.21 <sup>c</sup> (0.12) | 0.18 <sup>c</sup> (0.12) |  |
| Average (SD) proximity mid-channel <sup>d</sup> | 0.21 (0.24)              | 0.25 (0.20)              | 0.29 (0.26)              | 0.29 (0.20)              | 0.33 (0.17)              | 0.26 (0.25)              |  |
| % Forested                                      | 43.7 <sup>n.s.</sup>     | 33.7*                    | 37.9*                    | 49.4 <sup>n.s.</sup>     | 31.0*                    | 44.4 <sup>n.s.</sup>     |  |
| % Wetland                                       | 49.2 <sup>n.s.</sup>     | 45.6 <sup>n.s.</sup>     | 42.5 <sup>n.s.</sup>     | 48.8 <sup>n.s.</sup>     | 72.4*                    | 44.4 <sup>n.s.</sup>     |  |
| % Open water                                    | 9.4*                     | 18.4*                    | 26.4*                    | 2.3*                     | 0.0 <sup>n.a.</sup>      | 11.1*                    |  |

<sup>a</sup> SAV = submerged aquatic vegetation.

<sup>b</sup> Values of 1.00 indicate most upstream survey site and most upstream location.

<sup>c</sup> Values of 0.37 indicate most upstream survey site and 1.00, most upstream location.

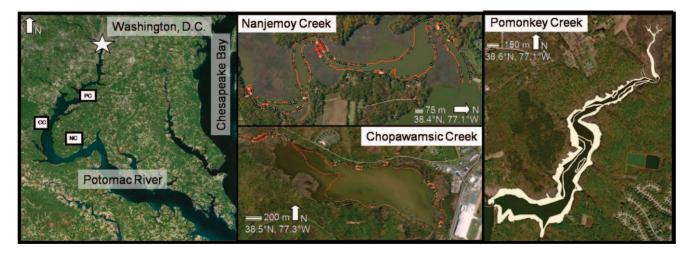
<sup>d</sup> Values of 1.00 indicate near the channel, with values near 0 indicating near shoreline.

Habitat attributes associated with position in the stream indicated similar locations among seasons. Snakeheads were generally caught near shorelines (< 30% of mid-channel distance from shore) and upper half of sampled stream (Table 1). More snakeheads were caught in the upper third of Chopawamsic Creek, as compared with Nanjemoy Creek where snakeheads were generally caught in the upper half of the stream. There was also little seasonal variation for in-stream locations relative to depth or SAV distribution (Table 1). Fish were captured in less than 2 m of depth (average = 0.7 m) for both Chopawamsic Creek and Nanjemoy Creek.

However, they were caught across a wider variety of depths in Nanjemoy Creek (SD range: 0.3–0.4) than Chopawamsic Creek (SD  $\sim$  0.2), where depth was less variable than in Nanjemoy Creek (Table 1). Fish were caught in or near SAV in Chopawamsic Creek, but less so in Nanjemoy Creek where SAV is less available.

## Habitat suitability criteria

Locations where snakeheads were clustered and locally abundant (i.e., hot spots) were identified for 380 total fish caught in Chopawamsic Creek and 231 fish caught in Nanjemoy Creek. These hot spots were evident



**Figure 2.** Northern snakehead *Channa argus* individuals were captured using boat electrofishing along or near the median track line (red line) in Chopawamsic Creek (CC; in 2010–2013), Nanjemoy Creek (NC; in 2013), and Pomonkey Creek (PC; in 2014), which are tidal freshwater streams tributary to the Potomac River (Chesapeake Bay watershed). Seasonal collections of adults (spring = green circular symbols; summer = yellow circular symbols; fall = orange circular symbols) in Chopawamsic Creek and Nanjemoy Creek were used to identify seasonal "hot spots" or regions where the fish was abundant or significantly clustered (90% confidence = tan; 95% confidence = orange; 99% confidence = red). The hot-spot data were used to help identify suitable habitat for Pomonkey Creek (tan shading).

**Table 2.** Locations where northern snakehead *Channa argus* individuals were captured in high abundance and clustered (i.e., hot spots) within Chopawamsic Creek (Chop; 2010–2013) and Nanjemoy Creek (Najy; 2013), tidal freshwater streams that are tributary to the Potomac River (Chesapeake Bay watershed). For each hot spot, some habitat characteristics were described for each season, including the cover of submerged aquatic vegetation (SAV), proximity to the most upstream end of the tidal stream (prox upstream), and proximity to the mid-channel (prox mid-chan). NA = data not available; — = not computed.

|   | Chop                     |                          |                       | Najy                     |                          |      |  |
|---|--------------------------|--------------------------|-----------------------|--------------------------|--------------------------|------|--|
|   | Spring                   | Summer                   | Fall                  | Spring                   | Summer                   | Fall |  |
| Hot-spot area (m <sup>2</sup> )                 | 39,400                   | 16,200                   | 2,000                 | 9,600                    | 10,600                   | 0    |  |
| Average (SD) depth (m)                          | 0.70 (0.34)              | 0.90 (0.10)              | 1.00 (—)              | 0.73 (0.36)              | 0.93 (0.36)              | NA   |  |
| Average (SD) proportion SAV                     | 0.05 (0.28)              | 0.17 (0.41)              | 0 (—)                 | 0.05 (0.23)              | 0.21 (0.15)              | NA   |  |
| Average (SD) proximity upstream                 | 0.63 <sup>a</sup> (0.27) | 0.54 <sup>a</sup> (0.29) | 0.75 <sup>a</sup> (—) | 0.28 <sup>b</sup> (0.13) | 0.22 <sup>b</sup> (0.12) | NA   |  |
| Average (SD) proximity mid-channel <sup>c</sup> | 0.71 (0.29)              | 0.71 (0.42)              | 1.00 (—)              | 0.80 (0.25)              | 0.96 (0.68)              | NA   |  |

<sup>a</sup> Values of 1.00 indicate most upstream survey site and most upstream location.

<sup>b</sup> Values of 0.37 indicate most upstream survey site and 1.00, most upstream location.

<sup>c</sup> Values of 1.00 indicate midstream location, with values near 0 reflecting closest shoreline locations.

for each season and stream (Figure 2), except fall for Nanjemoy Creek when the number of captures was low (N = 9). In Chopawamsic Creek, hot-spot clusters included relatively deeper sections of the stream (average depth 0.7-1.0 m) with a low cover of SAV (0-17%; Table 2), which are also attributes of upstream habitats that were identified as hot spots (Figure 2). Hot spots in Nanjemoy Creek included similar depths (0.7-0.9 m) and levels of SAV (5–21%). Hot-spot clusters generally included areas with low to moderate amounts of SAV (15-30% cover within the hot spot) and shallow to moderate depths (0.5-0.8 m). Although there was little difference in hot-spot characteristics among seasons (Table 2), fish tended to be found within 5 m of SAV in summer and fall (Figure 3). During spring, when SAV is beginning to grow, snakeheads were not highly associated with the occurrence of SAV (Figure 3).

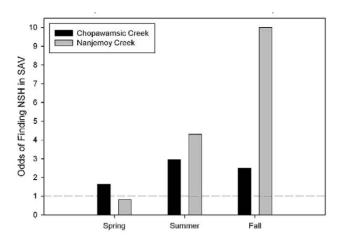
Inclusive of all seasons and both creeks, results from the probit regression analysis indicated that the probability of capturing a fish when there was no or intermediate SAV cover was greater than when there was complete SAV cover at a site (Table 3; Figure 4). The probability of occurrence depended on whether there was complete cover of SAV (coefficient = 0.38, P = 0.03), but not necessarily the presence of SAV (coefficient = -0.04, P = 0.81; Table 3). Position within the stream also significantly predicted the presence of snakehead (all sites and seasons, N = 693, log-likelihood = -373.3, P <0.0001; Table 3; Text S1, Table S2, Supplemental Material). Despite the level of SAV cover at a site, the probability of encountering snakehead decreased with proximity to mid-channel and increased with proximity to the most upstream, watered end (Figure 4). The probability of capturing snakehead was greatest within the upper 15% of a surveyed stream (Figure 4A), where more of the stream channel was sampled and where fish may have been more vulnerable to capture. The probability of capture was also highest within 30% of the mid-channel distance to shore. Much of the open-water habitat in Chopawamsic Creek was not surveyed (see Figure 2). More of the stream channel in upstream habitats was occupied than in downstream habitats (Figures 2 and 4), resulting in the significant interactions of proximity to mid-channel and proximity upstream (Table 3). Thus, using suitability indices, we identified suitability criteria as: 1) SAV edges that included 5 m SAV and 5 m adjacent open water; 2) less than 30% of mid-channel distance from either wetland or forested shorelines, areas which may or may not include SAV; and 3) the upper 15% of the surveyed stream.

#### **Population estimate**

Among mark-recapture periods when there were recaptures by researchers, the  $N_t$  averaged 91 adults (SD = 22.2) that were 494 mm total length (SD = 138; N)= 92) in lower Nanjemoy Creek, and 92 adults (SD = 36.9) that were 582 mm total length (SD = 119) in Chopawamsic Creek. Throughout the study, there were only 12 periods when fish marked during the initial sampling period were recaptured during the subsequent sampling event (7-14 d later). The recapture of marked fish provided data needed to estimate population size for each of the 12 periods (Table 4). For these periods, we excluded six tagged fish that had been harvested and reported by anglers within the mark-recapture period. Anglers generally harvested a low proportion of tagged snakehead in Chopawamsic Creek (26 of 393 tagged) and Nanjemoy Creek (4 of 251 tagged).

Using the mean and standard deviation of the population estimates, 10,000 possible  $N_t$  were randomly drawn from a normal distribution. The resulting  $N_t$ -90 was 140 adults for Chopawamsic Creek and 119 adults for Nanjemoy Creek. Using  $N_t$ -90, catch probability for both streams was low (Nanjemoy Creek: median q = 0.045; Chopawamsic Creek: median q = 0.046). The relatively low q estimates indicated that a low proportion of the adult population was being captured during each sampling event. Population size per hectare of suitable habitat (Nanjemoy Creek = 42.9 ha; Chopawamsic Creek = 50.5 ha) yielded a density of approximately three adults/ha for both streams.

The estimated suitable area in Pomonkey Creek was 14.6 ha (see Figure 2). With this area of suitable habitat and assuming a density of three adults/ha, the



**Figure 3.** Seasonal differences in the odds of collecting northern snakehead *Channa argus* within 5 m of submerged aquatic vegetation (SAV) within Chopawamsic Creek (March–October; 2010–2013) and Nanjemoy Creek (March–October 2013), which are tidal freshwater streams that are tributary to the Potomac River (Chesapeake Bay watershed).

 $N_t$  estimate was 44 adults for a biweekly period. The  $N_t$  estimate was not significantly different from an empirically derived  $N_t$  ( $N_t = 79$ , SD = 35.9; 95% confidence interval:  $13 \le N \le 148$ ), which was calculated from catch in Pomonkey Creek (CPH = 3.5, SD = 1.59, N = 4) and catch probability (average median q = 0.045). Interestingly,  $N_t$  predicted from total available aquatic habitat (43.6 ha) assuming three adults/ha was 131 and also did not differ significantly from  $N_t$  calculated by CPH and q.

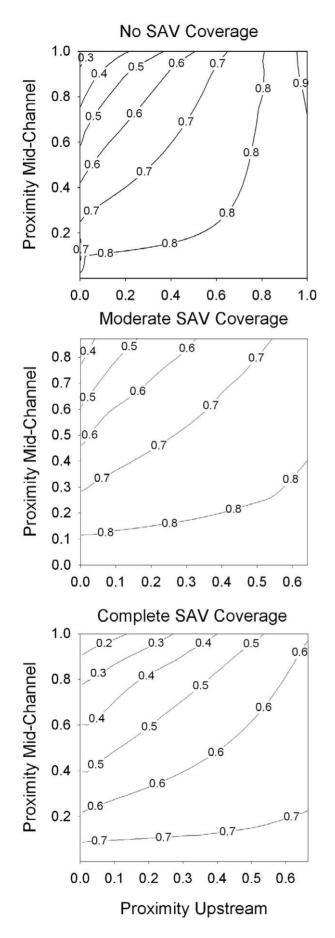
Using the habitat criteria established here, we identified approximately 7,093 ha of suitable habitat of 20,668 ha of habitat for snakehead in 44 major tidal freshwater tributaries of the Potomac River (Text 1, Figure S1, *Supplemental Material*). Assuming three adults/ ha, estimated adult population size was predicted to be 21,279 on the basis of suitable habitat.

#### Discussion

Habitat models are useful in fisheries management for setting goals in conservation and predicting population sizes of stream fishes (Fausch et al. 1988). Estimates of population size from suitable habitat models may be misleading when there is uncertainty in how habitat suitability is assigned and when density varies with spatial differences in exploitation (Fausch et al. 1988) or ideal free distributions for territorial animals (Fretwell and Lucas 1970; Kennedy and Gray 1993; Nicolai et al. 2014). Uncertainty in habitat suitability assignment and habitat use clearly depends on understanding complex specieshabitat relationships. Such relationships can be additionally obscured by variance in detectability, which is influenced by season and habitat conditions during sampling (Williams and Fabrizio 2011). This variance was minimized in this study by incorporating results widely reported in the literature, conducting in situ work across several seasons and two streams, and utilizing habitat metrics that are robust to sampling error. Conducting such work in numerous ecosystems can be exhaustive of time and resources. Here, habitat use and an estimated density of three fish/ha were similar between Chopawamsic Creek and Nanjemoy Creek. However, density of snakeheads has been observed to be as high as 25 fish/ ha in Little Hunting Creek, VA (J. Odenkirk, Virginia Department of Game and Inland Fisheries, personal communication). Therefore, our estimate of 44 adults for Pomonkey Creek could be an underestimate. In fact, a single day's collection in July (2014) amounted to 20 adults with boat electrofishing (J. Newhard, unpublished data). Future work will require estimating variance in density and incorporating that into extrapolated population sizes. In addition to providing variance for a population size estimate, information on density can also be used to set a conservation goal that lowers density in suitable habitat, a possible strategy for controlling biomass and spread of invasive species.

**Table 3.** For spring, summer, and fall seasons, occurrences of northern snakehead *Channa argus* among surveyed habitats (*N*) were examined relative to habitat factors using probit regression analyses for Chopawamsic Creek (2010–2013) and Nanjemoy Creek (2013), two tidal freshwater streams that are tributary to the Potomac River (Chesapeake Bay watershed). Coefficients are provided for predictors: proximity to the most upstream end of the stream (U), proximity to the mid-channel (M), the interaction of U and S (U × M), the presence or absence of submerged aquatic vegetation (SAV) within 78.5 m<sup>2</sup> of captures (SAV<sub>a</sub>), and complete or not cover of SAV (SAV<sub>b</sub>). Goodness of fit for models were compared using log-likelihoods (LL) and log-likelihood ratio(LLR) test statistics. Significance assumed when P < 0.05 and indicated with \*.

| Model       | N   | LLR   | LL     | U      | м      | $\mathbf{U} \times \mathbf{M}$ | SAVa  | SAV <sub>b</sub> |
|-------------|-----|-------|--------|--------|--------|--------------------------------|-------|------------------|
| All data    | 693 | 41.9* | -373.8 | -0.32  | -1.57* | 1.33*                          | -0.04 | 0.38*            |
| Chopawamsic | 387 | 39.2* | -177.6 | -1.25* | -1.29* | 1.12                           | 0.46* | 0.57*            |
| Spring      | 208 | 56.1* | -110.5 | -2.30* | -4.00* | 3.90*                          | 0.44  | 0.69*            |
| Summer      | 172 | 18.4* | -109.6 | -1.35  | -1.25  | 1.02                           | 0.43  | 0.48             |
| Fall        | 167 | 18.8* | -106.2 | -0.98  | -0.31  | -0.26                          | 0.50  | 0.62             |
| Nanjemoy    | 306 | 16.1* | -183.8 | -1.49  | -2.43* | 3.83*                          | -0.06 | 0.96*            |
| Spring      | 268 | 14.7* | -168.6 | -1.33  | -2.38* | 3.56*                          | 0.01  | 0.79             |
| Summer      | 126 | 7.1   | -64.4  | -2.91  | -2.64* | 5.56*                          | -0.05 | 4.14             |
| Fall        | 106 | 5.6   | -28.0  | -0.40  | -0.56  | -0.50                          | -0.72 | 4.26             |



**Table 4.** Northern snakehead *Channa argus* adults were marked (*M*) during periodic boat electrofishing surveys of Chopawamsic Creek and Nanjemoy Creek in the Potomac River (March–October). The creeks were subsequently surveyed (within 7–14 d) to record the numbers of caught fish (*C*) and caught fish that had been marked (*R*). The *M*, *C*, and *R* were used to provide a population estimate ( $N_t$ ) and its standard deviation (SD).

| Stream          | Year | Month  | м  | с  | R | N <sub>t</sub> | SD   |
|-----------------|------|--------|----|----|---|----------------|------|
| Chopawamsic Cr. | 2011 | May    | 15 | 15 | 1 | 128            | 64.6 |
| Chopawamsic Cr. | 2011 | June   | 15 | 12 | 3 | 52             | 16.7 |
| Chopawamsic Cr. | 2011 | June   | 12 | 11 | 1 | 78             | 37.8 |
| Chopawamsic Cr. | 2011 | July   | 11 | 6  | 1 | 42             | 18.7 |
| Chopawamsic Cr. | 2011 | July   | 21 | 9  | 1 | 110            | 54.2 |
| Chopawamsic Cr. | 2012 | May    | 11 | 16 | 2 | 68             | 26.7 |
| Chopawamsic Cr. | 2013 | June   | 14 | 18 | 1 | 143            | 72.4 |
| Chopawamsic Cr. | 2013 | July   | 18 | 11 | 1 | 114            | 56.8 |
| Nanjemoy Cr.    | 2013 | April  | 12 | 15 | 1 | 104            | 73.1 |
| Nanjemoy Cr.    | 2013 | May    | 12 | 10 | 1 | 72             | 48.6 |
| Nanjemoy Cr.    | 2013 | June   | 15 | 8  | 1 | 72             | 48.5 |
| Nanjemoy Cr.    | 2013 | August | 22 | 9  | 1 | 115            | 80.2 |

Our habitat suitability criteria for snakehead generally support those from other authors (Odenkirk and Owens 2005; Lapointe et al. 2010), but also provide additional insight in habitat use by this species. We demonstrated a greater preference for SAV in Nanjemoy Creek, where SAV was less available, than Chopawamsic Creek during summer and fall. If snakeheads are utilizing SAV to forage on prey fishes, then less common SAV patches in Nanjemoy Creek may aggregate prey fishes more distinctly and lead to greater use of those habitats by snakeheads. As SAV reached peak biomass in summer and fall, more snakeheads were collected in open-water areas, suggesting that use of those habitats may be likewise explained by the full development of SAV. It was unexpected that snakeheads were not captured in complete cover of SAV because of their preference for SAV habitat (Lapointe et al. 2010; Kumar et al. 2012). Dense SAV can be difficult to survey (Serafy et al. 1988) and capture efficiency via electrofishing may be greater at the edge than in the interior of SAV patches. However, it is not uncommon to capture largemouth bass Micropterus salmoides and other fishes in complete cover of SAV using boat electrofishing (pers. obs., J. Love). Interior patches of SAV may simply be avoided by snakeheads, a behavior that has been observed in

**Figure 4.** Probability of occurrence of northern snakehead *Channa argus* relative to proximity to the most upstream end and proximity to mid-channel for combined data sets from Chopawamsic Creek (2010–2013) and Nanjemoy Creek (2013), which are tidal freshwater streams that are tributary to the Potomac River (Chesapeake Bay watershed). Probabilities are provided for three levels of cover by submerged aquatic vegetation (SAV): no SAV, complete SAV cover, and an intermediate amount of SAV that ranges between complete absence and complete cover.

smallmouth bass *Micropterus dolomieu* because of reduced foraging opportunities (Miranda and Pugh 1997). Ancillary surveys throughout expansive SAV supported this alternative because those surveys resulted in very few captured snakeheads (J. Newhard; unpublished data). Open-water habitats with complete SAV coverage were excluded from the habitat model. Ultimately, this did not influence the population size estimate because calculating a population size from suitable habitat in Pomonkey Creek was statistically as effective as calculating population size from total aquatic habitat.

Snakeheads were commonly caught near shorelines and in the upper ends of tidal freshwater streams. Even though collections had amassed in the upper ends of tidal freshwater streams, there was no evidence of shoaling or corralling of fish. In most cases, only one or two fish were caught in a minute, which was followed by at least several minutes of survey that yielded no fish. Telemetry data support movement of a portion of the population into upstream habitats (particularly during spring; Lapointe et al. 2013), though it remains unclear whether movement occurs as a group or as individuals.

Snakehead control efforts may become more widespread if the species expands along the eastern coast of the United States (ANSTF 2014). Identifying suitable habitat and estimating potential population sizes will be beneficial to fishery managers tasked with controlling small populations and targeting removals. Waterways that are vulnerable to colonization or expansion may also be identified. Unfortunately, habitat use within nontidal water has not been well documented. Currently, small populations exist within tidal and nontidal waterways at John Heinz National Wildlife Refuge (Delaware River watershed), Potomac River National Wildlife Refuge complex, and Blackwater National Wildlife Refuge (Blackwater River watershed; Benson 2014). Habitat suitability criteria for snakehead may also lend insight into whether significant overlap of habitat occurs with species of concern, such as American shad Alosa sapidissima and striped bass Morone saxatilis, for federal agencies.

Snakeheads have not caused species extinctions and have not yet been implicated in population declines of other fishes in the Potomac River. The current decline in recruitment and catches of largemouth bass in Maryland's portion of the Potomac River has been largely attributed to declines in the distribution of SAV (MDDNR 2014). Large populations of snakeheads could theoretically have negative impacts on fisheries for largemouth bass (Love and Newhard 2012). Negative impacts may not be measured if harvest is sufficiently lowering snakehead biomass. There may also be a lag time before negative impacts are measured (Crooks 2005; Albins and Hixon 2008). To help prevent snakeheads from having negative impacts in the Potomac River drainage and the Chesapeake Bay watershed, angling pressure and agency removals have been aggressively encouraged since 2010. As fishes are harvested without regulation, population declines can occur (Myers et al. 1994) and modeling studies indicate that such declines can occur when a large proportion of the population is harvested (> 70%; Zipkin et al. 2009). The densities of snakeheads measured in Chopawamsic Creek and Nanjemoy Creek (three fish/ ha) are generally less than those for a sympatric top predator that is rarely harvested in the tidal Potomac River, largemouth bass. Expected density for largemouth bass in Maryland's streams in 1996 was 12 fish/ha (MDDNR 1996), but ranged from 1 fish/ha to 18 fish/ha in 2014 among sites electrofished for bass (J. Love, unpublished data). Thus, despite harvest, snakeheads may be more abundant than bass in some areas.

ArcGIS technology has the potential to utilize wellknown habitat relationships to manage a fishery and inform invasive species control plans. Hot spots were useful for defining habitat suitability criteria, which could ultimately lead to increased harvest rates and reduced economic costs to anglers or agencies involved with control efforts. The population size or biomass of an invasive species is an important metric in management, but can be challenging to determine. Quantifying the total area of suitable habitat for an exotic, potentially invasive species could reflect population size, if density in a subsample of suitable habitat is known. The area of suitable habitat can also more aptly assess the threat of establishment in light of the number of introductions (Lockwood et al. 2005) and the minimum size of the initial population needed for population growth (Stephens et al. 1999). Generating public interest by mapping suitable habitat, estimating population sizes, and identifying impacts can also help reinforce reasons to prevent introductions of nonnative species. To conserve financial resources and lessen the need for control and management of snakeheads, perhaps a more cost-effective approach would be to target the public with a message to prevent further releases to novel waters (Leung et al. 2002; Keller and Lodge 2007).

## **Supplemental Material**

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

**Text S1.** Supplemental text file. Metadata that details information for Table S1, Table 2, and Figure S1.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S1 (3 KB TXT).

**Table S1.** Date, latitude, longitude, and size (length and weight) of northern snakehead *Channa argus* captured between 2010 and 2013 (March–October) are presented for Nanjemoy Creek, Chopawamsic Creek, and Pomonkey Creek. For each fish, the tag number and sampling conditions are also noted (boat electrofishing voltage, pulses, amperage, and total sampling time [in seconds] for each date). Additionally, water temperature (°C), dissolved oxygen levels (mg/L), salinity, weather, and tide are noted for each date.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S2 (166 KB XLS).

**Table S2.** Habitat data used to predict presence (P or 1) or absence (A or 0) of northern snakehead (NSH) *Channa argus* within Nanjemoy Creek and Chopawamsic

Creek between 2010 and 2013 (March–October). For each season and stream, the presence (P or 1) or absence (A or 0) of wetland habitat, forest habitat, or open-water habitat is given. Additionally, the proportion of submerged aquatic vegetation (SAV) transformed by an arcsine square-root function and the rank of SAV is also given (2 = full cover at a site; 1 = intermediate cover at a site; 0 = absence). The location of each capture relative to the upstream end of the tidal stream, the distance of each capture to the mid-channel, and the proportional depth at each site relative to the deepest point of the stream are also given.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S3 (126 KB XLS).

**Figure S1.** A figure illustrating 44 major tributaries of the tidal Potomac River. The area of suitable habitat for Northern Snakehead *Channa argus* within each of these tributaries was extrapolated using ArcGIS from distribution and habitat data collected between 2010 and 2013 (March - October) in targeted tributaries.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S4 (17.6 MB JPG)

**Reference S1.** [ANSTF] Aquatic Nuisance Species Task Force. 2014. National Control and Management Plan for Members of the Snakehead Family (*Channidae*).

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S5; also available at http://www.anstaskforce. gov/Species%20plans/SnakeheadPlanFinal\_5-22-14.pdf (2311 KB PDF).

**Reference S2.** Benson AJ. 2014. Northern snakehead sightings distribution. http://nas.er.usgs.gov/taxgroup/fish/northernsnakeheaddistribution.aspx (August 2014).

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S6; also available at http://nas.er.usgs.gov/ taxgroup/fish/northernsnakeheaddistribution.aspx (2132 KB PDF).

**Reference S3.** Courtenay WR Jr., Williams JD. 2004. Snakeheads (Pisces, Channidae): a biological synopsis and risk assessment. U.S. Geological Survey Circular 1251.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S7 (21.8 MB PDF).

**Reference S4.** Fausch KD, Hawkes CL, Parsons MG. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. General Technical Report PNW-GTR-213. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S8 (2497 KB PDF).

**Reference S5.** [MDDNR] Maryland Department of Natural Resources. 1996. Study V: investigations of largemouth bass populations inhabiting Maryland's tidal waters. Federal Aid in Sportfish Restoration Project F-48-R. Annapolis, Maryland: Annual Report Maryland Department of Natural Resources.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S9 (5151 KB PDF) **Reference S6.** [MDDNR] Maryland Department of Natural Resources. 2014. Survey and management of Maryland's fishery resources: performance report 2013. Federal Aid in Sportfish Restoration Project F-48-R-9. Annapolis, Maryland: Annual Report Maryland Department of Natural Resources.

Found at DOI: http://dx.doi.org/10.3996/102014-JFWM-075.S10 (7476 KB PDF).

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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