TECHNICAL BRIEF

Management Brief on Diet and Consumption of Northern Snakehead *Channa argus*

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Abstract

Northern snakehead *Channa argus*, a species originating from Asia, was illegally introduced into ponds of Maryland in 2002. Later discovered in tidal freshwater of Potomac River, the species has become successfully established in many streams of Potomac River. We investigated prey preference and consumption rates of northern snakeheads from Potomac River (2014 – 2018). Snakeheads showed little preference towards a particular prey fish but fed opportunistically on prey that were common and widespread. Using a published model for snakehead consumption rates and Maryland habitat features, we estimated total annual consumption of prey for a typical size stream population of snakeheads in Potomac River as 2,118,947 grams (or 2.3 U.S. tons) of fish for the population per year. Applying published observations on the relative proportion of prey consumed to total consumption estimates, we learned that a typical size stream population of snakeheads could consume 40,797 banded killifish, 31,215 bluegill sunfish, 26,055 goldfish, 13,181 white perch, 9,176 largemouth bass juveniles and 7,112 yellow perch, per year. We further calculated that over 4.5 million prey fishes could be consumed per year for the 21,279 snakeheads that had been projected to inhabit suitable streams in Potomac River. We conclude that snakeheads have the potential to change aquatic communities by significantly altering abundance of relatively common fishes.

Introduction

Invasive aquatic species can cause ecological harm to biodiversity and economic hardships (Pimentel et al. 2005). Northern snakehead is an invasive, primarily fish-eating species that is native to Asia. It was introduced to temperate areas of North America in the early 2000s and has been considered a nuisance or invasive largely because of its life history properties (Courtenay and Williams 2004; ANSTF 2014). Some of these properties, such as size and predatory behavior, have been lauded by anglers who are eager to have another gamefish opportunity. Numerous initiatives have launched to encourage lowering population sizes of snakeheads via harvest (Love and Genovese, *in press*). The debate over protecting northern snakehead, however, has intensified as its population size increased from Potomac River in 2004 to the rest of the tidally influenced Chesapeake Bay watershed (Odenkirk and Owens 2005; Love et al. 2017). In spite of the positive benefits of having another species to fish, negative properties of the species include disease transmission (Iwanowicz et al. 2013) and competition with other piscivores when resources become limiting (Saylor et al. 2012). This has led to concerns for popular sport fisheries and in some areas, snakeheads are likely to have only a marginal, but potentially important negative effect on largemouth bass *Micropterus salmoides* fisheries (Love and Newhard 2012; Love et al. 2015). Perhaps more importantly, the role of northern snakehead as a predator of other fishes has not been rigorously assessed in aquatic ecosystems across its introduced range. The diet of northern snakehead includes a diversity of fishes (Saylor et al. 2012), but also crayfish, amphibians, and occasionally small mammals (unpublished data, JWL). In spite of the diet information from a few streams across its introduced range, little is known regarding prey preference and actual impacts from these ecosystems owed to predation. The objectives of this study were to determine prey preferences for northern snakehead and then, to estimate impacts on the ecosystem via total consumption from a typical population of snakeheads.

Methods

Lab Experiments – Prey Preference

We used ten experiments in a pond to examine prey preferences for northern snakehead. The pond was a lined, 0.10 hectare outdoor pond filled with water from a reservoir (Figure 1).

The pond was covered with a 50 millimeter mesh net to prevent bird or reptiles from entry. Structure was added to the pond, including buoys, floats, a 2 meters x 3 meters plastic structure, two nest boxes made of wood (1 meter x 1 meter) and two cinder blocks. Neither type nor number of structural elements changed throughout the experiments. The pond was aerated to provide dissolved oxygen during the experiment. Water temperature in the pond ranged between 20.6 degrees Celsius and 29.7 degrees Celsius, had low conductivity (224 - 290 microSiemens), and dissolved oxygen levels that ranged between 3.0 milligrams per liter and 11.5 milligrams per liter.

We completed the ten pond experiments between May and September (2014 – 2018) that included nine experiments with a single northern snakehead (or density = 10 fish/hectare) as the predator (570 – 715 millimeters) and a control experiment without a predator. We used a density of snakeheads in the experiment that was within realistic ranges observed from Potomac River (3 fish/ha and 12.5 fish/ha to 22 fish/ha; Love et al. 2015; Odenkirk and Isel 2017). The prey fish community differed slightly for each experiment (Table 1), but reflected diet data reported for twenty-five northern snakeheads that we examined from the Potomac River (unpublished data, JWL) and from Saylor et al. (2012) who reported that prey included sunfish, perch, topminnows and minnows, largemouth bass, and American eel *Anguilla rostrata*. We found that crayfish *Procambrus clarkii* was found in 32% of guts that we examined, but were not used as a prey source in this study.

Prior to introduction to the pond, all fish were measured for length and weight. For our experiments we used four types of prey: 1) spiny rayed fishes (yellow perch *Perca flavescens*; white perch *Morone americana;* juvenile largemouth bass; 50 – 150 millimeters); 2) sunfishes (pumpkinseed *Lepomis gibbosus*; bluegill *Lepomis macrochirus*; black crappie *Pomoxis* *nigricans*; 55 – 130 millimeters); 3) conspicuous water column dwellers (goldfish *Crassius auratus*; golden shiner *Notemigonus chrysoleucas*; 25 – 145 millimeters); and 4) top minnows or minnows (banded killifish *Fundulus diaphanus*; creek chubsucker *Erimyzon oblongus;* spottail shiner *Notropis hudsonius*; 40 – 110 millimeters). Amphibians (e.g., *Bufo americanus*), which are also potential prey items, could neither be enumerated nor prevented from entering the pond.

The prey fish community was exposed to an adult northern snakehead (570 – 715 millimeters) for approximately 14 days. During each two-week experiment period, the pond was routinely examined for serpents caught in netting, dead fish floating at the surface, and dissolved oxygen. Across all experiments, a sum of 25 dead prey fishes had been removed from the pond. These individuals, identified by species and length, were excluded from data analysis. After the experiment, the pond was drained and remaining prey fishes were evacuated to a catch box. These prey fishes were tallied and measured for length. The pond was flushed with water twice following each pond drain to ensure that all fishes were flushed out. When possible, prey fish were used again for experiments following at least a two-week recovery time in indoor tanks.

Prey preference from the pond experiments was determined using a modified Ivlev's electivity index (Ivlev 1961), which is the relative abundance of an eaten prey species compared to the relative availability of the prey species in the environment. This index has been criticized for its sampling bias, problems with unknown prey availability, and problems with identifying important prey in the gut because of differences in prey digestion (Straus 1979). These biases were reduced by controlling prey availability. Unaccounted prey items in the pond at the end of the experiment were assumed to have been eaten. To help meet that assumption, we flushed ponds twice and tried to prevent predation by terrestrial predators. A control experiment that included only fish prey species yielded 96% recovery of fish (Table 1).

Ivlev's electivity index (E) was calculated as:

$$E = {r_i - p_i}/{r_i + p_i}$$

where r_i is percent composition eaten for prey *i* and p_i is percent composition available for prey *i*.

Field Experiments – Prey Preference

We examined prey preference from field surveys by plotting the relationship between percentage of snakehead stomachs with a specific prey fish by the percentage of field survey sites containing that prey fish. The percentage of field survey sites containing a particular prey fish was determined from Maryland's annual Tidal Bass Survey (Love 2011). Prey fish were surveyed from 54 shorelines (250 meters long) that were randomly chosen from a pool of all possible shoreline locations in mainstem and tributary streams of Maryland's portion of tidal freshwater in Potomac River (September – November; 2018). Each shoreline was sampled using boat electrofishing settings that were appropriate for tidal freshwater (Smith-Root 5.0 or 9.0 gas-powered pulsator boat, 60 or 120 pulses per second) following protocols established by the Tidal Bass Survey's Standard Operating Procedure. The proportion of surveyed shorelines with a particular prey species was calculated from the Tidal Bass Survey, with one exception. This survey underestimated the occurrence of killifish (*Fundulus diaphanous*, *F. heteroclitus*), an important prey item for snakeheads because the boat electrofishing gear is often unable to target shallow, nearshore areas where the species occurs. Therefore, the percent occurrence of killifish among sites sampled using a beach seine survey (30.5 meters x 1.24 meters, bagless with 6.4 millimeter bar mesh) was determined from data collected by Maryland's Juvenile Striped Bass Seine Survey (Durell and Weedon 2017).

The percentage of snakehead stomachs with a particular prey fish was determined by analyzing data of Saylor et al. (2012) who had identified contents for 76 snakehead stomachs between April and October in 2007. Snakeheads had been caught from embayments and creeks of Potomac River, from both Maryland and Virginia shores (Saylor et al. 2012). For each prey species, the percentage of snakehead stomachs that had consumed at least one individual of the prey species was calculated. By plotting the relationship between the percentage of sites with a prey fish (x-axis) and percentage of stomachs with the prey fish (y-axis), we determined if prey preference was a function of the prey species' distribution among tidal freshwater habitats. The time span separating these studies was eleven years and we assumed that the ranked order of prey fish distribution had not changed significantly. A Spearman's Rank Correlation analysis between the factors was performed. A correlation that did not significantly differ from 0 would support the null hypothesis that snakehead prey preference was not influenced by the distribution of prey.

Analysis – Total Annual Consumption

Maximum consumption rate (C_{max}) for a fish was determined using a water temperature and size dependent model (Liu et al. 1998). The consumption rate model was:

$$\ln C_{max} = -6.718 + 0.522*\ln(W) + 0.440*T - 0.0077*T^2$$

where T is water temperature (degrees Celsius) and W (grams) is mass of the fish.

The vector of water temperatures used to calculate consumption rate were obtained from monthly water temperature (January 25 – December 10, 2018) measurements recorded approximately 1.8 meters below surface using a Yellow Springs Instrument sonde deployed by the Eyes on the Bay Program.

In order to generate weight and demographic data for a typical population, populations were surveyed by boat electrofishing surveys that targeted snakeheads from spring through summer (Smith-Root 5.0 or 9.0 gas-powered pulsator; amperage = 120 pulses per second) for three streams of Potomac River: Pomonkey Creek (2014-2015), Chopawamsic Creek (2010-2013), and Nanjemoy River (2013). Total lengths for 939 individuals were recorded and grouped into 100 mm bin ranges for each stream. Because of high variability in length-at-age (Gascho-Landis et al. 2011; Odenkirk et al. 2013), these length ranges do not represent age cohorts. Instead, length ranges represented a populations' size structure by 100 mm increments, which correspond with approximate growth rates between ages one and four for young northern snakeheads (total lengths 145 – 782 millimeters; Table 2).

Consumption rate for a fish of average mass within the length range was calculated for a day with an average monthly water temperature. This consumption rate was then extrapolated for the fish per month, the time scale to which water temperature was measured, by multiplying C_{max} by the number of days (d) in each month (i). This was done for the average mass computed for each length range (j) in the population. The C_{max} per month, per length range (j) was multiplied by the number of fish within the length range (n_j). The number of fish within a length range was determined by multiplying the proportion of fish expected in the length range and each hypothetical population abundance (N = 300 – 650, increment = 50). The proportion of fish expected in the length range was calculated from a linear model fit to the greatest value in the length range (independent variable) and proportions of fish observed in the length range as determined for the three surveyed populations (as above; dependent variable). Because some streams were surveyed multiple years, a median proportion was taken across years for each population prior to analysis (Table 2). The proportions predicted from the linear model were interpreted as an average size structure for populations within Potomac River.

Total annual consumption for the abundance of fish ($C_{max\text{-}N}$) was summed across months and across length ranges for each hypothetical population abundance as,

$$C_{max-N} = \sum_{i}^{i=12} \sum_{j}^{j=7} C_{max} * d_i * n_j$$

We determined C_{max-N} for each hypothetical abundance based on stream population sizes reported for northern snakehead from Potomac River (Odenkirk and Isel 2016). A Monte Carlo randomization routine was used to simulate 1000 runs of the model and compute an average C_{max-N} for the species. Each iterative run of the model included values of water temperature and mass that varied within the natural limits observed within a month and length range, respectively. In this way, we incorporated natural variation in water temperature and mass, which enabled us to produce an additive variance estimate for C_{max-N} at each population size tested here. Additionally, we translated C_{max-N} into the expected abundance of principal prey items consumed. The relative proportion of prey items (r_i; by weight from Saylor et al. 2012) was multiplied by C_{max-N}, and the product was divided by the average mass (W) of the prey species used in mesocosm experiments (from above) to translate mass to an approximate abundance. Prey items included: white perch (r = 0.091, W = 14.62 grams), yellow perch (r = 0.173, W = 51.50 grams), bluegill (r = 0.203, W= 13.77 grams), goldfish (r = 0.086, W = 7.00 grams), banded killifish (r = 0.092, W = 4.78 grams), and largemouth bass (r = 0.104, W = 24.00 grams). The translated prey abundance is only a relative approximation because it is based on average prey size used here. For instance, abundance would decline if average prey size increased, and vice versa. The translation merely provided a more universally understood concept for total consumption.

Results

Prey Preference

There was no evidence of strong prey preferences for northern snakehead. The low levels of electivity during mesocosm experiments demonstrated that common prey items are most frequently consumed (Fig. 2). Conspicuous prey items available in the mesocosm experiments, such as goldfish and golden shiner, were only slightly preferred in some experiments (E = 0.41 – 0.56, experiment #1, #5, #6, #8). There was likewise little preference for streamlined, spiny rayed fish (E = 0.56, experiment #8), broad bodied sunfishes (E = 0.41, experiment #8), or killifish and minnows (E = 0.40, experiment #9). Supporting these results, we found a significantly positive relationship between percentage of stomachs with prey fish and percentage of sites with prey fish in Potomac River (Spearman's Rank Correlation Coefficient = 0.770; Fig. 3). Widespread prey species, such as banded killifish, bluegill and yellow perch, were most frequently identified from stomachs of northern snakehead. Based on these assessments, we conclude that prey consumption was related to the relative availability of prey in environment rather than any preference for a species or species group.

Consumption

Consumption rates (C_{max}) predicted by the model ranged between 0 to 115.82 milligrams prey per gram of snakehead per day and showed a bimodal distribution. Consumption rates for colder monthly water temperatures (average = 5.46 degrees Celsius) were predicted to be lower (average C_{max} = 0.61, standard deviation = 0.53) than those when monthly water temperature was warmer (average = 21.0 degrees Celsius; average C_{max} = 18.95; standard deviation = 15.81). After summing consumption rates among months and across length ranges, total annual consumption ($C_{max\text{-}N}$) for a population of 600 northern snakeheads, an estimate that reflects that for an established population in Little Hunting Creek (Potomac River; Odenkirk and Isel 2016), was estimated as 2,118,947 grams (standard deviation = 32,129) or 2.3 U.S. tons of prey for the population per year (Fig. 4). Each additional snakehead added to the population was expected, on average, to increase total annual consumption by 3,504 grams or 7.7 pounds of prey per snakehead per year (Fig. 4, upper panel). Total consumption per year for a population of 600 northern snakeheads could result in consumption of 40,797 banded killifish (194,943 g), 31,215 bluegill sunfish (430,146 g), 26,055 goldfish (182,229 g), 13,181 white perch (192,824 g), 9,176 largemouth bass juveniles (220,370 g), 7,112 yellow perch (366,577 g) and 531,858 grams of other organisms. Of these, bluegill, goldfish, and banded killifish were expected to be most numerous in stomachs for snakeheads collected from Potomac River (Fig. 4, lower panel). We conclude that a population of 600 snakeheads could consume at least 127,538 (standard deviation = 913) fishes per year, including both game fish and non-game fish. When assuming a population size of 21,279 snakeheads in Potomac River, which was estimated by Love et al. (2015) using habitat suitability modeling, at least 4,547,312 (standard deviation = 69804) fishes could be consumed per year by the population in Potomac River.

Discussion

Northern snakeheads can be characterized as generalized opportunists foraging across multiple trophic levels within an ecosystem. Prey items consumed, but not evaluated during this study, included amphibians and crustaceans. Even though our results indicated little prey preference, Weber et al. (2010) demonstrated that generalist predators could elicit preferences because of prey availability and handling time. Scientists have routinely shown that largemouth bass commonly consume broad-bodied fishes, such as gizzard shad and sunfishes, as well as minnows (Shoup and Wahl 2009; Saylor et al. 2012). A diet study for northern snakehead has also suggested similar preferences (Saylor et al. 2012). Our study indicates these preferences may simply be owed to prey availability (Reid et al. 1999; Shoup and Wahl 2009) or ease of consumption (Hambright 1991), rather than innate preference (Ghedotti et al. 1995). Prey availability can change over time, though, and relative abundance of major prey fish species has varied over the past decade in our surveys with a coefficient of variation of at least 64%. Furthering the understanding of how snakeheads assume an ecological role in ecosystems and how that role changes over time with prey availability could be explored with stable isotope analysis and continued prey preference work.

Consumption rates computed for northern snakeheads ranged widely depending on water temperature and averaged 18.95 milligrams of prey per gram of predator per day during warmer water temperatures (6.6 degrees Celsius to 28.7 degrees Celsius). For smallmouth bass, Vigg et al. (1991) also found that consumption rates were more than double in warmer months of July and August than April through June. Consumption rates were comparable to averages reported for North American predaceous fishes such as smallmouth bass (28.7) and walleye (14.2) from impounded water of Columbia River (Vigg et al. 1991). Consumption rates predicted from Liu et al. (1998) produced values for the Potomac River population within realistic ranges for other populations of primarily fish-eating or piscivorous fishes.

Water temperature and fish mass were used to predict consumption rate, but other factors can also be important and were not considered here. In addition to water temperature, consumption rates can vary with water clarity. Smallmouth bass had significantly greater consumption rates in clear water than in water where turbidity approached 40 NTU (Carter et al. 2010). Habitat complexity also affects consumption rates. Suitability models for northern snakehead suggest seasonal affiliation with complex, submerged structure (Lapointe et al. 2010;

Love et al. 2015). Using a series of controlled experiments, Godinho and Ferreira (2006) reported largemouth bass consumed fewer sunfish and minnows when submerged vegetation was present. Additionally, neither prey preference nor consumption modeling here addressed consumption of crayfish. In 2015 and 2016, 11 of 57 dissected snakeheads (or 19 percent) from Potomac River had eaten crayfish. Eating crayfish could reduce average consumption rates of snakeheads if it increases handling times as it does for largemouth bass (Hoyle and Keast 1987). Because bioenergetics modeling did not include crayfish as prey (Liu et al. 1998), it is currently unknown how much consumption rate would be affected by consuming crayfish or how much snakeheads could impact crayfish populations. In general, handling times, habitat complexity and clarity and optimal conditions for foraging and growth by northern snakehead are not well-known for snakeheads from Potomac River. None-the-less, these results demonstrate that snakeheads could negatively impact populations of fish prey by lowering their abundance.

The role of an aquatic predator in a food web can be described by its size, its ability to swim and chase prey, its ability to capture prey, its ability to consume a diversity of prey sizes, and its efficiency in converting energy to mass or reproduction. Effective predators can change an aquatic community by changing abundances of its organisms (Jackson et al. 2001; Frank et al. 2005; Pimentel et al. 2005; Goudswaard et al. 2008). Because of a snakehead's diet, lack of obvious prey preferences, and consumption rates similar to other piscivorous fishes in North America, we generally conclude that northern snakehead could significantly impact aquatic communities via predation. Compensatory responses of the aquatic community are possible and Chesapeake Bay ecosystems widely differ in habitat complexity and quality. Therefore, we strongly recommend research into how aquatic community diversity and abundance change in areas proliferated by snakeheads.

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Literature Cited

ANSTF (Aquatic Nuisance Species Task Force). 2014. National Control and Management Plan for Members of the Snakehead Family (Channidae). (https://www.anstaskforce.gov/Documents/Snakehead_Control_and_Management_plan_Final_Approved-May2015.pdf). 80 pp.

Carter, M.W., D.E. Shoup, and J.M. Dettmers. 2010. Effects of turbidity and cover on prey selectivity of adult Smallmouth Bass. Transactions of the American Fisheries Society 139:353-361.

Courtenay, W.R., Jr. and J.D. Williams. 2004. Snakeheads (Pisces, Channidae)-A biological synopsis and risk assessment. United States Geological Survey Circular 1251, Denver, Colorado.

Durell, E.Q. and C. Weedon. 2017. Striped Bass Seine Survey Juvenile Index Web Page. Dnr.maryland.gov/fisheries/Pages/juvenile-index.aspx. Maryland Department of Natural Resources, Fishing and Boating Service, Annapolis.

Frank, K.T., B. Petrie, J.S. Choi, and W.C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621-1623.

Gascho Landis, A.M., N.W.R. Lapointe, P.L. Angermeier. 2011. Individual growth and reproductive behavior in a newly established population of northern snakehead (*Channa argus*), Potomac River, USA. Hydrobiologia 661:123-131.

Ghedotti, M.J., J.C. Smihula, and G.R. Smith. 1995. Zebra mussel predation by round gobies in the laboratory. Journal of Great Lakes Research 21:665-669.

Godinho, F.N. and M.T. Ferreira. 2006. Influence of habitat structure on the fish prey consumption by Largemouth Bass, *Micropterus salmoides*, in experimental tanks. Limnetica 25: 657-664.

Goudswaard, K.P.C., F. Witte, and E.F.B. Katunzi. 2008. The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. Environmental biology of Fishes 81:127-139.

Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. Transactions of the American Fisheries Society 120:500-508.

Hoyle, J.A. and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Canadian Journal of Zoology 65:1972-1977.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, U.S.A.

Iwanowicz, L., C. Densmore, C. Hahn, and P. McAllister. 2013. Identification of largemouth bass virus in the introduced northern snakehead inhabiting the Chesapeake Bay watershed. Journal of Aquatic Animal Health 25: 191-196.

Jackson, D.A., P.R. Peres-Neto, and J.D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157-170.

Jackson, D.A. 2002. Ecological effects of *Micropterus* introductions: The dark side of black bass. Pages 221-234 *in* D.P. Philipp and M.S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Lapointe, N., J. Thorson, and P. Angermeier. 2010. Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac river system. Ecology of Freshwater Fish 19:566-577.

Liu, J., Y. Cui, and J. Liu. 1998. Food consumption and growth of two piscivorous fishes, the mandarin fish and the Chinese snakehead. Journal of Fish Biology 53:1071-1083.

Love, J.W. and P. Genovese. *In Press*. Fishing for an invasive: Maryland's toolbox for managing Northern Snakehead fisheries. American Fisheries Society Symposium.

Love, J.W. 2011. Habitat suitability index for largemouth bass in tidal rivers of the Chesapeake Bay watershed. Transactions of the American Fisheries Society 140:1049-1059.

Love, J.W. and J.J. Newhard. 2012. Will the expansion of Northern Snakehead negatively affect the fishery for Largemouth Bass in the Potomac River (Chesapeake Bay)? North American Journal of Fisheries Management 32:859-689.

Love, J.W. and J.J. Newhard. 2018. Expansion of northern snakehead in the Chesapeake Bay watershed. Transactions of the American Fisheries Society 147:342-349.

Love, J.W., J.J. Newhard, and B. Greenfield. 2015. A geospatial approach for estimating suitable habitat and population size of the invasive northern snakehead. Journal of Fish and Wildlife Management 6:145-157.

Love, J.W., J.J. Newhard, and M. Groves. 2015. Risk of population decline for Largemouth Bass in a Potomac River fishery (USA): Effects from invasive Northern Snakehead. Pages 207-222 *in* M.D. Tringali, J.M. Long, T.W. Birdsong, and M.S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Nuñez, M.A., S. Kuebbing, R.D. Dimarco, and D. Simberloff. 2012. Invasive species: to eat or not to eat, that is the question. Conservation Letters 5:334-341.

Odenkirk, J.S. and M.W. Isel. 2016. Trends in abundance of northern snakeheads in Virginia tributaries of the Potomac River. Transactions of the American Fisheries Society 145:687-692.

Odenkirk, J.S. and S. Owens. 2005. Northern snakeheads in the tidal Potomac River system. Transactions of the American Fisheries Society 134:1605-1609.

Odenkirk, J.S., C. Lim, S. Owens, and M. Isel. 2013. Insight into age and growth of northern snakehead in the Potomac River. North American Journal of Fisheries Management 33:773-776.

Pimentel, D., R. Zuniga, D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

Reid, S.M., M.G. Fox, and T.H. Whillans. 1999. Influence of turbidity on piscivory in Largemouth Bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 56:1362-1369.

Saylor, R.K., N.W.R. Lapointe, and P.L. Angermeier. 2012. Diet of non-native Northern Snakehead (*Channa argus*) compared to three co-occurring predators in the lower Potomac River, U.S.A. Ecology of Freshwater Fish 21:443-452.

Shoup, D.E. and D.H. Wahl. 2009. The effects of turbidity on prey selection by piscivorous Largemouth Bass. Transactions of the American Fisheries Society 138:1018-1027.

Shoup, D.E. and D.W. Wahl. 2009. The effects of turbidity on prey selection by piscivorous Largemouth Bass. Transactions of the American Fisheries Society 138:1018-1027.

Strauss, R.E. 1979. Realiability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by Northern Squawfish, Walleyes, Smallmouth Bass, and Channel Catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:421-438.

Weber, M.J., J.M. Dettmers, D.H. Wahl, and S.J. Czesny. 2010. Effects of predator-prey interactions and benthic habitat complexity on selectivity of a foraging generalist. Transactions of the American Fisheries Society 139:1004-1013.

Table 1. Northern snakehead of various total lengths (in millimeters) consumed a fraction of prey available for dated pond experiments. A control experiment was conducted in July 2014 to compute the difference in number of prey fish when a snakehead was not added to pond.

Experiment	Start Date	# Prey Avail.	# Prey Eaten	Days	Total Length
1	6/2/2014	28	4	14	660
2	7/2/2014	28	13	14	N/A[1]
3	7/23/2014	30	3	14	625
4	8/28/2014	25	7	18	620
5	6/4/2015	33	12	14	600
6	6/22/2015	25	5	14	570
7	7/13/2015	37	3	14	600
8	8/13/2017	20	14	17	570
9	5/5/2018	48	23	24	715
Control	7/31/2014	29	28	15	none

[1]Snakehead measurement not available.

Table 2. Ranges of total lengths (in millimeters) of northern snakehead (*Channa argus*) used to compute consumption rates. For each range, an average mass for fish (in grams) was calculated with variance represented as standard deviation in parentheses. The proportion of individuals in each length range was predicted using linear regression and a dataset of observed proportions from three populations in Potomac River (Chopawamsic Creek, Nanjemoy Creek, Pomonkey Creek).

Total Length	Average Mass	Predicted Proportion
150 – 249	109.0 (30.8)	0.1887
250 – 349	239.5 (79.9)	0.1705
350 – 449	580.6 (149.6)	0.1523
450 – 549	1242.4 (238.2)	0.1341
550 – 649	1986.8 (326.7)	0.1159
650 – 749	3248.0 (477.9)	0.0977
750 – 849	4530.2 (611.6)	0.0795
850 – 949	6279.6 (414.3)	0.0613

Figure 1. Picture of pond used for mesocosm experiments to examine prey preferences of northern snakehead *Channa argus* in Maryland.

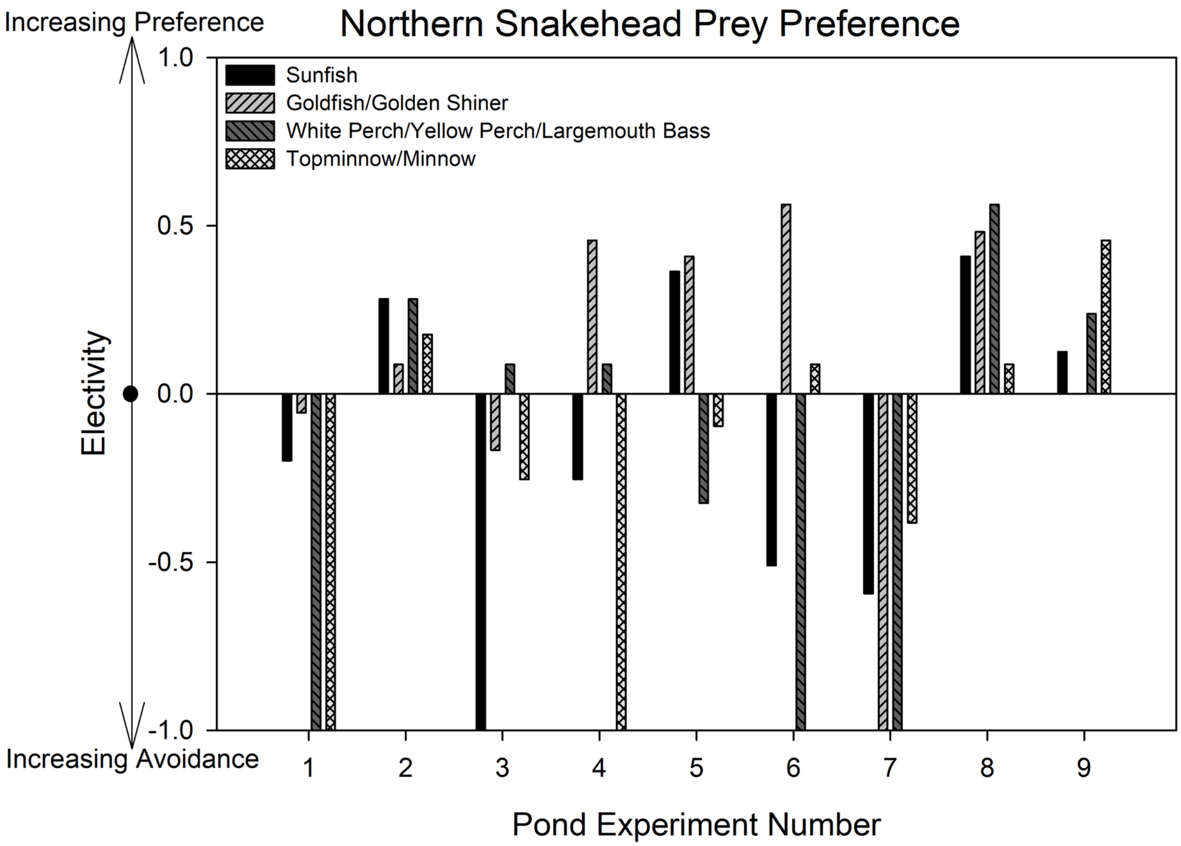

Figure 2. Northern snakehead *Channa argus* did not show strong prey electivity (i.e., preference) for any prey species group consistently across pond experiments.

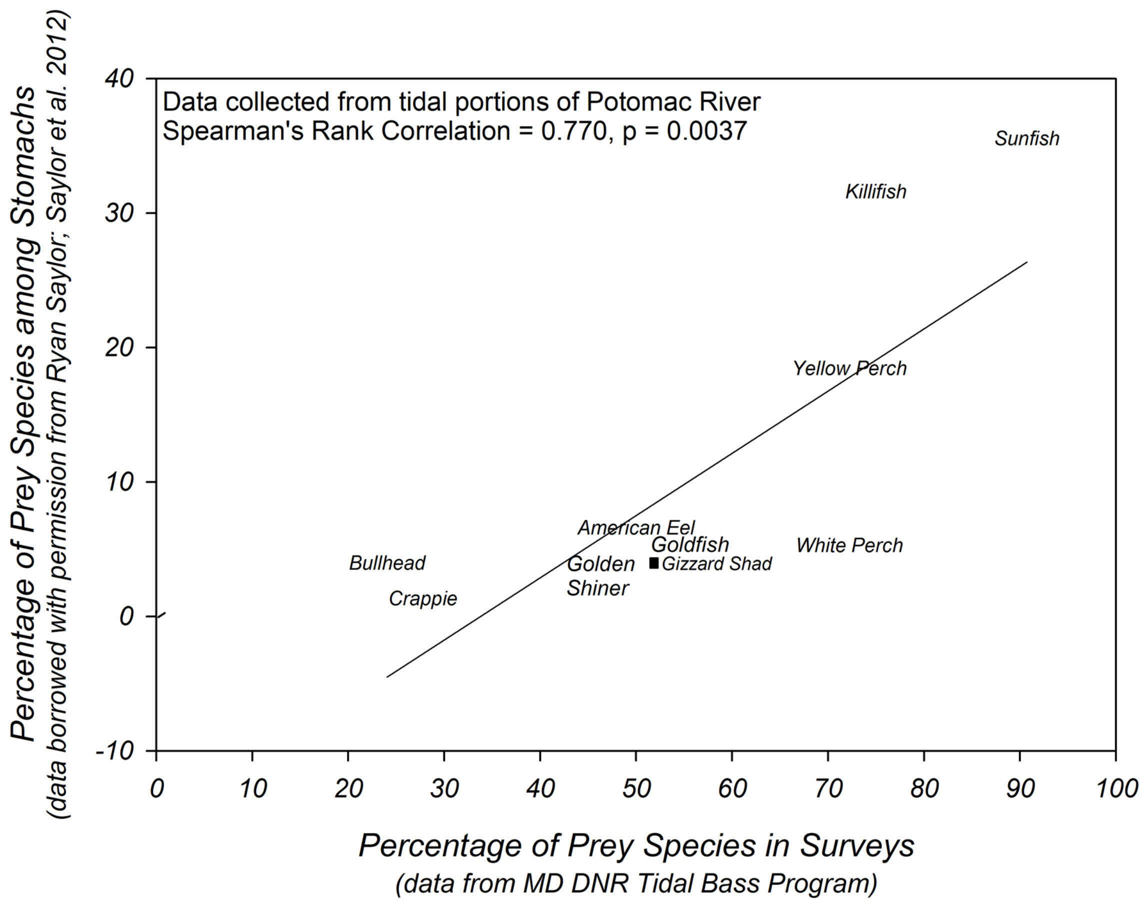

Figure 3. Percentages of sites with fish prey species from Potomac River tidal freshwater habitats (Maryland) increase with percentages of northern snakehead *Channa argus* stomachs containing that fish prey species. Most symbols were represented by species name; black rectangle represents Largemouth Bass.

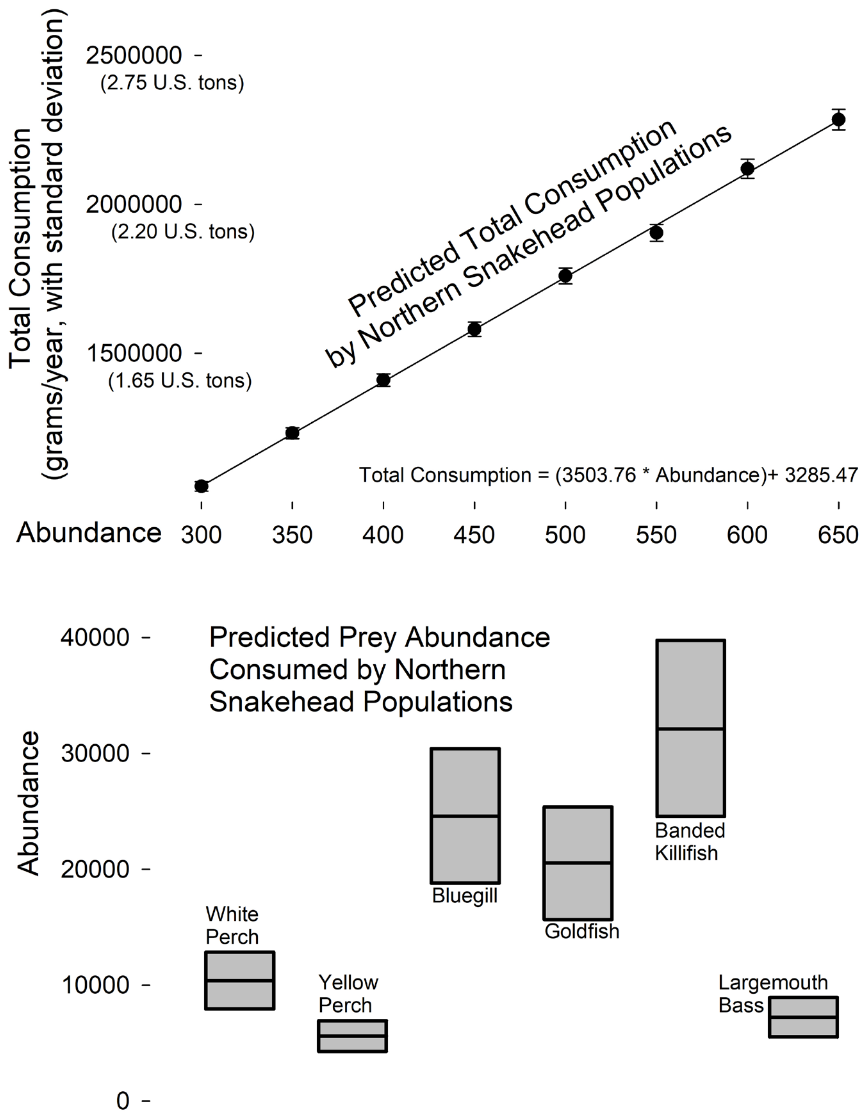

Figure 4. Upper Panel: Predicted total consumption by northern snakehead *Channa argus* increases with its abundance. Lower Panel: Amount of prey consumed by northern snakehead, as predicted from total consumption and relative proportions of prey found in stomach contents. Horizontal lines in boxes represent medians bounded by lower 25th and upper 75th percentiles for all abundance levels examined here (300 to 650 snakeheads).