This is the accepted version of the following article: Love, J.W. and J.J. Newhard. 2021. Using Published Information to Predict Consumption of Northern Snakehead *Channa argus* in Maryland. Transactions of the American Fisheries Society, which has been published in final form at <u>https://doi.org/10.1002/tafs.10306</u>.

## 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 Maryland rivers. Deleterious effects owed to Northern Snakehead introductions are unresolved. To add some insight into potential impacts of snakeheads, we calibrated a previously published, temperature-dependent maximum consumption model using measured population densities and size structure from three streams in Potomac River (2010 - 2015) and Maryland monthly water temperatures. We then informed the results of the model using diet and prey preference data from previously published studies and field and outdoor pond studies (2014 - 2018). The total annual maximum consumption estimated from the model for a population of 600 snakeheads, a size estimate approximated from published population sizes in streams of Potomac River, amounted to 2,189 kg of fish for the population per year. We found no evidence of strong prey preferences and therefore, partitioned total annual consumption to relative proportions of prey fishes observed for Northern Snakehead. We estimated total annual maximum consumption for a population as: 661 kg/yr of sunfishes Lepomis spp., 522 kg/yr of Yellow Perch Perca flavescens, 332 kg/yr of Goldfish Crassius auratus, 250 kg/yr of White Perch Morone americana, and 174 kg/yr of Banded Killifish *Fundulus diaphanus*. While these maximum consumption levels are not likely fully realized in nature owed to constraints on physiological capacities and prey hiding, they do indicate that Northern Snakehead is a formidable predator. We highlight our methodology to assess potential impacts as snakeheads expand their range and conclude that, as indicated by earlier risk assessments, Northern Snakehead's opportunism and consumption of significant

biomasses of some recreationally and commercially important species of fish make it an important predator in Maryland's ecosystems.

## Introduction

Invasive aquatic species can cause ecological harm to biodiversity and economic hardships (Pimentel et al. 2005). Northern Snakehead *Channa argus*, a species native to Asia, primarily eats fish and following its introduction to temperate areas of North America in the early 2000s, is considered a nuisance or invasive species because of its life history traits (Courtenay and Williams 2004; ANSTF 2014). The species has increased in relative abundance by 10- to 100-fold since introduction in streams tributary to Potomac River, the second largest river of the Chesapeake Bay watershed, the largest coastal estuary in North America. Since its introduction, the species has either maintained or slightly decreased in relative abundance in those streams (Odenkirk and Isel 2016), but has spread rapidly throughout the Chesapeake Bay watershed (Love and Newhard 2018). It has gained abundance despite numerous initiatives to encourage lowering population sizes via harvest (Love and Genovese 2019). Negative consequences of this expansion include transmission of Largemouth Bass Virus by Northern Snakehead (Iwanowicz et al. 2013) and possible competition with existing sportfish, Largemouth Bass *Micropterus salmoides* (Love and Newhard 2012; Saylor et al. 2012; Love et al. 2015).

Predatory exotic species can have significant impacts on ecosystems by reducing prey biomass and influencing species diversity; in extreme cases, exotic aquatic predators have elicited strong declines in abundance and changes in aquatic community structure (Pycha and King 1975; Awiti 2011; Gallardo et al. 2016), constituting a major disturbance to an ecosystem. The ecological disturbance that Northern Snakehead has caused North American ecosystems has not been widely studied across its introduced range, leaving unresolved whether there are deleterious effects owed to introduction (Orth 2019). Effects may be widespread in the ecosystem, however, because Northern Snakehead forages on a wide range of fishes (Saylor et al. 2012) and crayfish and amphibians (pers. obs., JWL; Isel and Odenkirk 2019).

Our goal was to use published information to predict total annual maximum consumption of Northern Snakehead on various prey species in tidal freshwater habitats of Maryland's Potomac River (Chesapeake Bay watershed). Snakeheads have been rumored to consume mainly topminnows (e.g., *Fundulus diaphanus*) and small sunfishes (e.g., *Lepomis macrochirus*), and have also been rumored to consume everything in an ecosystem including sportfish (e.g., *Micropterus salmoides*). The objectives of this study were: 1) to parameterize a published temperature-dependent consumption model (Liu et al. 1998) using data obtained from Potomac River; and 2) to inform results of the model using published studies of diet (Saylor et al. 2012; Isel and Odenkirk 2019), which we also measured using field and outdoor pond studies.

#### Methods

## **Consumption Model**

We determined maximum consumption rate  $(C_{max})$  using a water temperature and size dependent model developed from snakeheads fed *ad libitum* (Liu et al. 1998). The model was:

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

where T is water temperature (°C) and W (g) is the weight of the fish. This model was parameterized with data for monthly water temperature and weight for specific length groups.

In order to calculate consumption rate, we used monthly water temperature (January 2018 – December 2018) measurements recorded approximately 1.8 m below surface using a Hydrolab Surveyor 4a/5 (MDDNR 2018; see *Supplemental Material* S1). These data were averaged from four locations with recent long-term water temperature data ranging from January to December

for tidal freshwater in Potomac River (Figure 1; see also, eyesonthebay.dnr.maryland.gov). One of the stations occurred in a major tributary of Potomac River, while the other three were in the mainstem. Water temperatures included in the model ranged between 2.2 °C and 28.5 °C, a range similar to that of other Potomac River tributaries (USGS 2020). Our results are bounded by the range used here for each month (*Supplemental Material* S1).

We generated average weights for length classes from Northern Snakehead boat electrofishing surveys from spring through summer (Smith-Root 5.0 or 9.0 gas-powered pulsator; current = 5 - 10 amps, frequency = 120 pulses per second) for three streams of Potomac River: Pomonkey Creek (2014 - 2015), Chopawamsic Creek (2010 - 2013), and Nanjemoy River (2013; Figure 1). Total lengths (mm) and weights (g) for 939 individuals collected from these streams were recorded during field surveys. Total length ranged between 152 mm – 885 mm. Weight ranged between 0.03 kg – 6.70 kg. For analysis, we grouped lengths into 100 mm bin ranges for each stream. Length ranges do not represent age cohorts, which should instead be determined using otoliths (Gascho-Landis et al. 2011; Odenkirk et al. 2013). Weight was averaged for each length range with its standard deviation (Table 2).

We calculated maximum daily consumption rate for a fish of average weight within the length range with an average monthly water temperature. This consumption rate was then extrapolated for the fish to month by multiplying  $C_{max}$  by the number of days (d) in each month (*i*). This was done for the average weight computed for each length range bin (*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<sub>j</sub>). The n<sub>j</sub> was determined by multiplying the proportion of fish expected in the length range bin by hypothetical population abundances (N = 300 – 650, increment = 50), which represented a range of population sizes reported for Northern Snakehead from a stream in

Potomac River (Newhard et al. 2019). The proportions of fish expected in the length range bin were calculated by fitting a linear model to a relationship of length bin (independent variable) and proportions of fish observed in the length range bin for three surveyed populations from Potomac River (as above; dependent variable). Some streams were surveyed multiple years and a median proportion was taken across years for each population prior to analysis. Because the sampling gear under-represented the abundance of younger Northern Snakehead during surveys, we used proportions predicted from the linear model (a = 0.239, b = -0.000182,  $r^2 = 0.24$ , p = 0.02) to estimate n<sub>i</sub> (Table 2).

Total annual maximum consumption for the abundance of fish  $(C_{max,N})$  was extrapolated to a year and population by summing across months and across length range bins,

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

We determined  $C_{maxN}$  for each abundance level, but highlighted values for a population size of 600, which was similar to the greatest abundance reported by Odenkirk and Isel (2016) for Little Hunting Creek (Figure 1). The population from Little Hunting Creek was used because of its time series of reported abundances. It also represents a stream that is similar to other lesser studied freshwater streams of the Potomac River. A Monte Carlo randomization routine was used to simulate 1,000 runs of the model and compute an average  $C_{maxN}$  for the species. Each iterative run of the model included values of water temperature and weight 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 weight, which enabled us to produce an additive variance estimate for  $C_{maxN}$  at each population size tested here.

# **Diet Studies**

We determined the  $C_{max}$  for each of the principal prey items consumed by Northern Snakehead. Principal prey items were identified from Saylor et al. (2012) and these data were further corroborated using field studies of diets for 57 Northern Snakehead adults from the Potomac River (unpublished data, JWL; see *Supplemental Material* S2). The prey and the relative proportion of each fish prey genus (r; by weight) as reported by Saylor et al. (2012) was: American Eel *Anguilla rostrata* (r = 0.0222), bullheads *Amerius* spp. (r = 0.0007), killifishes *Fundulus* spp. (r = 0.0780), Gizzard Shad *Dorosoma cepedianum* (r = 0.0266), Golden Shiner *Notemigonus chrysoleucas* (r = 0.0319), Goldfish *Cyprinus auratus* (r = 0.1510), Largemouth Bass *Micropterus salmoides* (r = 0.0204), sunfishes *Lepomis* spp. (r = 0.3020), crappies *Pomoxis* spp. (r = 0.0133), White Perch *Morone americana* (r = 0.1143), and Yellow Perch *Perca flavescens* (r = 0.2386). Of these, Goldfish, Largemouth Bass, and Bluegill (*Lepomis macrochirus*) have been introduced into Maryland waters.

Species do not appear to be consumed based upon preference or electivity (Isel and Odenkirk 2019), but to further support those observations, we used ten experiments in a pond study. The pond was a lined, 0.10 ha outdoor pond filled with water from a reservoir and was covered with a 50 mm mesh net to prevent bird or reptiles from entry. We added habitat features to the pond, including buoys, floats, a 2 m x 3 m plastic structure, two nest boxes made of wood (1 m x 1 m) 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 °C – 29.7 °C, with conductivity that ranged 224  $\mu$ S – 290  $\mu$ S, and dissolved oxygen levels that ranged between 3.0 mg/L – 11.5 mg/L.

We completed pond experiments between May and September (2014 - 2018). Each outdoor pond experiment lasted 14 days – 24 days, with four experiments conducted in 2014,

three experiments in 2015, one experiment in 2017 and one experiment in 2018 (Table 1). After each experiment, the pond was drained and remaining prey fishes were evacuated to a catch box. We tallied survivors and measured them for total length. There were nine experiments with a single Northern Snakehead (density = 10 fish/ha) as the predator (570 mm – 715 mm) and a control experiment without a predator. To ensure that we used a density consistent with field observations, we used a density of snakeheads in the experiment that ranged between 3 fish/ha – 22 fish/ha, which was the observed range from Potomac River (Love et al. 2015; Odenkirk and Isel 2016).

Prey species used in the experiment reflected the species reportedly eaten by Northern Snakehead in the Potomac River. Prior to introduction to the pond, the total length (mm) and weight (g) of prey fish were measured. For analysis, prey fish species were further aggregated into fish groups to help improve sample size numbers in each group: Group 1) broad bodied, spiny-rayed fishes (BSp; Black Crappie Pomoxis nigricans (110 mm); Bluegill Lepomis *macrochirus* (56 mm – 125 mm); Bluespotted Sunfish *Enneacanthus gloriosus* (55 mm – 61 mm); Green Sunfish L. cyanellus (90 mm - 111 mm); Pumpkinseed L. gibbosus (65 mm - 130 mm)); Group 2) fusiform, spiny-rayed fishes (FSp; Largemouth Bass (80 mm – 125 mm); White Perch (45 mm – 120 mm); Yellow Perch (50 mm – 145 mm)); Group 3) golden soft-rayed fishes (GSo; Goldfish Crassius auratus (50 mm – 113 mm); Golden Shiner Notemigonus chrysoleucas (45 mm – 140 mm)); and Group 4) other soft-rayed minnows or killifishes (OSo; Banded Killifish Fundulus diaphanus (32 mm – 110 mm); Creek Chubsucker Erimyzon oblongus (90 mm – 110 mm); Mummichog F. heteroclitus (40 mm – 75 mm); Spottail Shiner Notropis hudsonius (95 mm – 100 mm)). Amphibians (e.g., Bufo americanus), which are also potential prey items, could neither be enumerated nor prevented from entering the pond.

We calculated prey preference using a modified Ivlev's electivity index (Ivlev 1961). The index is the relative abundance of an eaten prey species compared to the relative availability of the prey species in the environment (i.e., experimental pond). This index has been criticized for its sampling bias because of 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 using outdoor pond experiments with a known community of prey fishes. We assumed prey items not accounted for at the end of the experiment were eaten. To help meet that assumption, we monitored and flushed ponds and prevented predation by terrestrial predators by using wildlife netting to cover the ponds. Across all experiments, 25 dead prey fishes were removed from the pond. These individuals, identified by species and length, were excluded from data analysis. The pond was flushed with water twice following each experiment to ensure that all fishes were flushed out. We also conducted a control experiment without a predator to determine the level of mortality (Table 1). We recovered 96% of the fish from the control experiment and did not adjust prey numbers for predatory experiments.

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. The E was calculated for each of the nine pond experiments for each of four fish groups created because of similar morphology. The value  $r_i$  was determined by dividing the number of prey consumed within each of the four prey fish groups by the total number of prey consumed among groups. The value  $p_i$  was determined by dividing the total number of prey available within each of the four prey fish groups by the total number of prey available within each experiment was the preference of a prey fish group by Northern Snakehead relative to the prey fish groups' availability in the prey fish community. We plotted *E* for each group and each pond experiment. Strong electivity was indicated by values close to 1.0 (strong preference) or -1.0 (strong avoidance). Weak electivity was indicated by values close to 0.0. For the purpose of our study, we noted moderate to strong prey preferences for a group when values ranged between 0.5 – 1.0. Box plots of *E* for each prey group were also generated with quartiles to determine whether median values ranged between 0.5 – 1.0. To test whether *E* differed from zero for each prey group, we determined the 95% upper confidence limit (UCL) and 95% lower confidence limit (LCL) of *E* for each prey fish group. When zero was included in the interval between limits, we concluded that mean *E* did not differ from zero.

### Results

Maximum consumption rates ( $C_{max}$ ) predicted by the temperature-dependent consumption model ranged between 0.05 mg – 62.27 mg prey per gram of snakehead per day. Maximum consumption rates for colder monthly water temperatures were predicted to be lower (average = 4.6 °C; average  $C_{max} = 0.44$ , standard deviation = 0.33) than those when monthly water temperature was warmer (average = 19.4 °C; average  $C_{max} = 18.17$ ; SD = 16.17). Across months and length ranges, total annual maximum consumption ( $C_{max,N}$ ) ranged between 1,093 kg/yr – 2,371 kg/yr depending on population size (Figure 2). Each additional snakehead added to the population was expected, on average, to increase total annual maximum consumption by 3.6 kg of prey per year (Figure 2). Assuming a population size of 600 Northern Snakehead, we determined that total annual maximum consumption was 2,189 kg/yr.

There was no evidence of strong preference for a prey species from outdoor pond experiments (Figure 3). Conspicuous gold colored, soft rayed minnows were moderately preferred by Northern Snakehead in one (E = 0.56) of nine experiments. There was also moderate preference for fusiform, spiny rayed fish (E = 0.56) in one of the experiments. No experiments had moderate to high E values for broad bodied spiny-rayed fishes and for other soft-rayed minnows or topminnows. For most prey groups, the median E was near zero or slightly less than zero (Figure 2). On average, E did not differ from zero for any prey fish group (mean, 95% LCL & 95% UCL; BSp: -0.15, -0.53 & 0.22; GSo: 0.08, -0.29 & 0.46; FSp: -0.23, -0.71 & 0.25; OSo: -0.21, -0.60 & 0.18).

Using published diet information, total annual maximum consumption per year was partitioned by multiplying relative proportion with total consumption for a population size of 600 individuals. We estimated that a population of 600 individuals could annually consume 661 kg/yr of sunfishes *Lepomis* spp., 522 kg/yr of Yellow Perch *Perca flavescens*, 332 kg/yr of Goldfish *Crassius auratus*, 250 kg/yr of White Perch *Morone americana*, and 174 kg/yr of Banded Killifish *Fundulus diaphanus* (Figure 4A). Total consumption for any prey species varied with population size of Northern Snakehead (Figure 4B).

### Discussion

Northern Snakehead can be characterized as a generalized opportunistic species, eliciting little innate prey fish preferences, and foraging on many ecologically and morphologically divergent species within an ecosystem. Similar to that suggested by Isel and Odenkirk (2019), our study indicates little prey preference by Northern Snakehead. The commonness of prey in the diet of Northern Snakehead could be owed to prey availability (Reid et al. 1999; Shoup and Wahl 2009), or perhaps ease of eating (Hambright 1991; Weber et al. 2010). The type of prey could affect how easily it is eaten. For example, consumption of crayfish could increase handling times as it does for Largemouth Bass (Hoyle and Keast 1987). In 2015 and 2016, 11 of

57 (or 19%) dissected Northern Snakehead adults from Potomac River had eaten crayfish. The species consumed by Northern Snakehead are common in tidal freshwater of the Chesapeake Bay estuary (Murdy et al. 1997) and are also common in the diet of another opportunistic predator in Potomac River, Largemouth Bass (Saylor et al. 2012). Predation on these species by Northern Snakehead could affect community structure like Largemouth Bass (Jackson 2002) but the intensity of impact likely depends on predator population size (this study) and compensatory reproduction or behaviors by prey species.

We estimated maximum consumption levels using a model developed from fish fed ad *libitum* (Liu et al. 1998) but natural consumption levels would be lower (Armstrong and Schindler 2011). Predators forage at levels lower than 75% of their physiological capacity (Armstrong and Schindler 2011) and those levels can be further limited by environmental factors, such as water temperature, water clarity, and habitat complexity. Daily changes in water temperature, for example, affect consumption rates (Liu et al. 1998) and these changes can vary in magnitude and duration among ecosystems. Consumption rates possibly slow during summer when water temperatures exceed thermal optima and energy is expended more frequently during facultative air breathing (Gascho Landis et al. 2011). However, fish may reduce energy expenditures by acclimatizing to seasonally harsh conditions (Love and Rees 2002) or adapting their behavior. We have observed Northern Snakehead during warm summer months burrowing into sediment in shallow water, possibly a means for achieving thermal optima during summer. Total consumption could also be affected by ecosystem-dependent water clarity levels (Carter et al. 2010) and habitat complexity (Godinho and Ferreira 2006). Smallmouth Bass had significantly greater consumption rates in clear water than in water where turbidity approached 40 NTU (Carter et al. 2010). Godinho and Ferreira (2006) also reported Largemouth Bass

consumed fewer sunfish and minnows in the presence of submerged vegetation, which is a seasonal habitat association for Northern Snakehead as well (Lapointe et al. 2010; Love et al. 2015). Actual annual consumption will therefore vary from that reported here and whether scientists observe changes in relative abundance of prey species after introduction of Northern Snakehead depends on habitat conditions in the ecosystem and predator population size.

The range of sizes for Northern Snakehead used to model consumption by Liu et al. (1998; 45 g – 546 g) included juveniles and adults, but did not include maximum body sizes considered here (33 g – 6698 g), leading us to extrapolate beyond their original consumption rate model. Consumption rates estimated here for Northern Snakehead were comparable to averages reported for North American predaceous fishes such as Smallmouth Bass (28.7 mg/g/d) and Walleye *Sander vitreus* (14.2 mg/g/d) from impounded water of Columbia River (Vigg et al. 1991). None-the-less, a fishs' metabolic rate can decrease with size if the fish becomes more efficient in activity or respiration (Post and Lee 1996). This could ultimately reduce total annual maximum consumption levels for a population. We did not observe that general weight accumulation declined with increasing total length (see *Supplemental Material* S3), but encourage more research on the inflection points for biphasic metabolism and consumption rates of large adult Northern Snakehead.

We highlight a methodology to assess potential impacts as snakeheads expand their range and conclude that, as indicated by earlier risk assessments (Courtenay and Williams 2004), Northern Snakehead is an important predator in Maryland ecosystems because of opportunism and consumption of significant biomasses of several recreationally and commercially important fish species. In spite of appreciable levels of total annual maximum consumption, it appears unlikely that snakeheads are actually consuming at levels that threaten to cause the extirpation of abundant prey species in tidal Potomac River. The prey species noted here have not become extirpated since introduction of snakeheads (unpublished data, JWL). However, ecosystems naturally differ in productivity and effects of additive natural mortality will differ among species. Community level consequences of Northern Snakehead introduction have varied between negligible (Isel and Odenkirk 2019) to significant (Newhard and Love 2019). Introduced predators can alter community structure through predation (Jackson et al. 2001; Jackson 2002; Frank et al. 2005; Pimentel et al. 2005; Goudswaard et al. 2008) and Northern Snakehead indiscriminately preys upon aquatic fishes and across multiple trophic levels (Saylor et al. 2012; Isel and Odenkirk 2019; this study). Newhard and Love (2019) noted a change in aquatic community structure in Blackwater River (Maryland) following the introduction of Northern Snakehead. Their results differed from Isel and Odenkirk (2019) who found relative abundances of some prey populations were relatively unchanged following the introduction of Northern Snakehead. The differences in these studies may be explained by abundance of Northern Snakehead and resiliency and diversity of the prey populations, as well as environmental differences between ecosystems. The level of invasiveness of Northern Snakehead likely depends on the ecosystem and we strongly recommend research into assessing the resiliency of aquatic communities for multiple ecosystems to further our understanding of Northern Snakehead impacts in North America.

### Acknowledgements

The authors wish to thank biologists with the Maryland Department of Natural Resources Freshwater Fisheries Program for their help in conducting the project, specifically Mary Groves, Branson Williams, Tim Groves and Ross Williams. The authors also wish to thank Ryan Saylor and Duane Chapman, who both provided data and early comments for this manuscript. The authors also thank those who helped fund the project including Austin Murphy with the Potomac Snakehead tournament and U.S. Fish and Wildlife Service (Sport Fish Restoration (Dingell-Johnson) Act, CFDA#15.605). The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

## References

- ANSTF (Aquatic Nuisance Species Task Force). 2014. National Control and Management Plan for Members of the Snakehead Family (Channidae). www.anstaskforce.gov/Documents/Snakehead\_Control\_and\_Management\_plan\_Final\_A pproved-May2015.pdf. 80 pp. Reference R1.
- Armstrong, J.B. and D.E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature 476:84-88.
- Awiti, A.O. 2011. Biological diversity and resilience: lessons from the recovery of cichlid species in Lake Victoria. Ecology and Society 16: 1-9.
- 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. Reference R2.
- Frank, K.T., B. Petrie, J.S. Choi, and W.C. Leggett. 2005. Trophic cascades in a formerly coddominated ecosystem. Science 308:1621-1623.
- Gallardo, B., M. Clavero, M.I. Sánchez, and M. Vilà. 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22:151-163.

- 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.
- 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.
- Isel, M.W. and J.S. Odenkirk. 2019. Evaluation of Northern Snakehead diets in Virginia's tidal rivers and lakes. Pages 83-93 *in* J.S. Odenkirk and D.C. Chapman, editors. Proceedings of the first international snakehead symposium. American Fisheries Society, Symposium 89, Bethesda, Maryland.
- 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. 2019. Fishing for an invasive: Maryland's toolbox for managing Northern Snakehead fisheries. Pages 139-152 *in* J.S. Odenkirk and D.C. Chapman, editors. Proceedings of the First International Snakehead Symposium. American Fisheries Society, Symposium 89, Bethesda, Maryland.
- 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.
- Love, J.W. and B.B. Rees. 2002. Seasonal differences in hypoxia tolerance in gulf killifish, *Fundulus grandis* (Fundulidae). Environmental Biology of Fishes 63:103-115.
- MDDNR (Maryland Department of Natural Resources). 2018. Quality Assurance Project Plan for the Maryland Department of Natural Resources Chesapeake Bay Water Quality
   Monitoring Program – Chemical and Physical Properties Component for the period July
   1, 2018 – June 30, 2019. Annapolis, Maryland. Reference R3.
- Murdy, E.O., R.S. Birdsong, and J.A. Musick. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, D.C.
- Newhard, J.J., J.S. Odenkirk, L. Lyon. 2019. Effects of fishing on select populations of Northern Snakehead in the Potomac River. Pages 159-171 *in* J.S. Odenkirk and D.C. Chapman, editors. Proceedings of the first international snakehead symposium. American Fisheries Society, Symposium 89, Bethesda, Maryland.

- Newhard, J.J. and J.W. Love. 2019. Comparison of fish community within the Blackwater River watershed before and after establishment of Northern Snakehead *Channa argus*. U.S. Fish and Wildlife Office, Maryland Fish and Wildlife Conservation Office, Annapolis.
- 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., 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.
- Orth, D.J. 2019. Socrates opens a Pandora's box of Northern Snakehead issues. Pages 203-224 *in*J.S. Odenkirk and D.C. Chapman, editors. Proceedings of the first internationalsnakehead symposium. American Fisheries Society, Symposium 89, Bethesda, Maryland.
- 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.
- Post, J.R. and J.A. Lee. 1996. Metabolic ontogeny of teleost fishes. Canadian Journal of Fisheries and Aquatic Sciences 53:910-923.
- Pycha, R.L. and G.R. King. 1977. Changes in the lake trout population of southern Lake
  Superior in relation to the fishery, the sea lamprey, and stocking, 1950-70. Technical
  Report 28, Great Lakes Fishery Commission, Great Lakes Science Center. Reference R4.
- 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.W. Wahl. 2009. The effects of turbidity on prey selection by piscivorous Largemouth Bass. Transactions of the American Fisheries Society 138:1018-1027.
- Snakehead Terror. 2004. Snakehead Terror. Image Entertainment, RLJ Entertainment, an AMC Network Company, Silver Spring, Maryland.
- Strauss, R.E. 1979. Reliability 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.
- USGS (U.S. Geological Survey). 2020. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation), accessed December 17, 2020, at URL https://waterdata.usgs.gov/md/nwis/current/?type=qw&group\_key=basin\_cd
- 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. For dated pond experiments (2014 – 2018), Northern Snakehead *Channa argus* of various total lengths (mm) were added to ponds with a certain number of available prey (# Prey Avail.) for a certain number of days (Days) and remaining prey (# Prey Remain) were counted at the end of the experiment. Outdoor pond experiments were conducted in Brandywine (Maryland) at a regional field station operated by Maryland Department of Natural Resources. A control experiment was conducted in July 2014 to compute the difference in number of prey fish when a Northern Snakehead was not added to pond.

Table 2. Estimated population structure for Northern Snakehead *Channa argus* estimated from data collected for three populations in Potomac River (Chopawamsic Creek, Nanjemoy Creek, and Pomonkey Creek) surveyed in 2010 – 2015. For various total length (mm) ranges for Northern Snakehead, average mass for fish (g) with standard deviation (in parentheses) was calculated for use in a temperature-dependent consumption model. The predicted proportion of individuals in each length range was predicted using linear regression of observed proportions in length ranges for three populations in Potomac River (Chopawamsic Creek, Nanjemoy Creek, Pomonkey Creek).

Figure 1. Map of Potomac River highlighting major streams tributary (labeled thumbtacks) to the mainstem that drains to the Chesapeake Bay (see inset). Black dots represent four locations where water temperature was measured during our study.

Figure 2. Relationship of model predictions for total annual maximum consumption (kg/yr) by Northern Snakehead *Channa argus* scaled to simulated abundances.

Figure 3. Electivity indices (i.e., preference) for Northern Snakehead *Channa argus* for prey fish groups for each experiment (upper) and summarized with box plots (lower). Prey species were grouped into: BSp - broad bodied, spiny-rayed fishes (Black Crappie *Pomoxis nigricans*;

Bluegill *Lepomis macrochirus*; Bluespotted Sunfish *Enneacanthus gloriosus*; Green Sunfish *L. cyanellus*; Pumpkinseed *L. gibbosus*); FSp - fusiform, spiny-rayed fishes (Largemouth Bass; White Perch *Morone americana*; Yellow Perch *Perca flavescensi*); GSo - golden soft-rayed fishes (Goldfish *Crassius auratus*; Golden Shiner *Notemigonus chrysoleucas*); and OSo - other soft-rayed minnows or topminnows (Banded Killifish *Fundulus diaphanus*; Creek Chubsucker *Erimyzon oblongus*); Mummichog *F. heteroclitus*; Spottail Shiner *Notropis hudsonius*). Box plots include medians bounded by a lower 25<sup>th</sup> and an upper 75<sup>th</sup> percentiles for outdoor pond experiments conducted at a regional field station for Maryland Department of Natural Resources in Brandywine (Maryland) in 2014 - 2018.

Figure 4. Box plot of prey biomass consumed by Northern Snakehead, as predicted from total consumption and relative proportions of prey found in stomach contents (upper; A). Horizontal lines in boxes represent medians bounded by lower 25<sup>th</sup> and upper 75<sup>th</sup> percentiles for all abundance levels examined here (300 to 650 snakeheads). Total consumption for a commonly consumed subset of prey fishes was also plotted with various population sizes of Northern Snakehead (lower, B). Represented prey included: American Eel (*Anguilla rostrata*), sunfishes (*Lepomis* spp.), Bullhead (*Amerius* spp.), Crappie (*Pomoxis* spp.), killifishes (*Fundulus* spp.), Gizzard Shad (*Dorosoma cepedianum*), Golden Shiner (*Notemogonus chrysoleucas*), Goldfish (*Crassius auratus*), Largemouth Bass (*Micropterus salmoides*), White Perch (*Morone americana*), and Yellow Perch (*Perca flavescens*).

*Supplemental Material* S1. Monthly water temperature data (in °C) collected from four water quality monitoring stations on Potomac River (Maryland) and measured at approximately 1.8 m within the river. Date of sampling, time of sampling, and depth (in m) of measurement are

provided the latitude (in decimal degrees) and longitude (in decimal degrees) of each monitoring station.

*Supplemental Material* S2. Diets and sizes of fifty-seven northern snakeheads that were examined from three locations within Potomac River (Indian Head or lower Mattawoman Creek, upper Mattawoman Creek, and Pomonkey Creek; Maryland). Prey were identified, measured (in mm) and weighed (in g), when possible.

*Supplemental Material* S3. Total lengths (in mm) and weights (in g, when available) for Northern Snakehead *Channa argus* collected from various locations (given as latitude and longitude in decimal degrees) in three streams of Potomac River that were surveyed between 2010 – 2015: Pomonkey Creek (Maryland), Nanjemoy Creek (Maryland), and Chopawamsic Creek (Virginia). NA = data not available.