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PRIMARY RESEARCH PAPER

Individual growth and reproductive behavior in a newly established population of northern snakehead (*Channa argus*), Potomac River, USA

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Abstract Northern snakehead (*Channa argus*) were first found in the Potomac River in 2004. In 2007, we documented feeding and reproductive behavior to better understand how this species is performing in this novel environment. From April to October, we used electrofishing surveys to collect data on growth, condition, and gonad weight of adult fish. Growth rates of young were measured on a daily basis for several weeks. Mean length-at-age for Potomac River northern snakehead was lower than for fish from China, Russia, and Uzbekistan. Fish condition was above average during spring and fall, but below average in summer. Below-average condition corresponded to periods of high spawning activity. Gonadosomatic index indicated that females began spawning at the end of April and continued through August. Peak spawning occurred at the beginning of June when average temperatures reached 26°C. Larval fish growth rate, after the transition to exogenous feeding, was 2.3 (SD ± 0.7) mm (total length, TL) per day. Although Potomac River northern snakehead exhibited lower overall growth rates when compared to other populations, these fish demonstrated plasticity in timing of reproduction and rapid larval growth rates. Such life history characteristics likely contribute to the success of northern snakehead in its new environment and limit managers' options for significant control of its invasion.

Keywords *Channa argus* · Gonadosomatic index · Virginia · von Bertalanffy

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Introduction

Fisheries managers and aquatic conservationists face a continual onslaught of non-native fish introductions to inland waters of the United States (Fuller et al., 1999; Rahel, 2000). The first population of northern snakehead (*Channa argus*) in an open system in North America was documented in 2004 in the Potomac River (Odenkirk & Owens, 2005). Continued evaluation of the population using boat electrofishing

Table 1 Mean total length-at-age for fish capture from China, Uzbekistan, Amur River Basin, and the Potomac River (this study)

Body of water	Fish length (mm) at age						
	1	2	3	4	5	6	7
Huanghua Lake, China (Wu et al., 1999)	229	396	509	586	637		
Chimkurgan reservoir, Uzbekistan (Amanov, 1974)	207	313	375	491	559	623	671
Amur River, Russia (Nikolskiy 1956, from Amanov, 1974)	225	336	461	554	615	676	
Potomac River, USA	220 (31)	304 (76)	373 (80)	430 (99)	529 (103)	577 (52)	

One standard deviation indicated in parentheses

showed an increase in catch per unit effort from 0.2 fish/h in 2004 to 6.1 fish/h in 2006 (Odenkirk & Owens, 2007). While the total impact of this introduction is yet unknown, potential for negative effects on native aquatic communities is large (Courtenay & Williams, 2004). Adult northern snakehead are highly piscivorous (Ling, 1977). Introductions of predatory fish can alter aquatic community structure and food webs through top-down mechanisms (Madenjian et al., 2002). Northern snakehead have broad environmental tolerances, and have the potential to significantly impact aquatic resources throughout North America (Herborg et al., 2007).

Northern snakehead have a large global distribution. They are native to eastern Russia and China, as well as parts of North Korea (Courtenay & Williams, 2004). Former Soviet Republics of Uzbekistan, Kazakhstan, and Turkmenistan have experienced relatively recent introductions of northern snakehead (Amanov, 1974; Dukravets & Machulin, 1978). Northern snakehead introduction into the Aral Sea basin occurred in the early 1960s (Usmanova, 1982) and other range expansions occurred in the mid-1980s (Dukravets, 1992).

Knowledge of natural history and ecological characteristics of newly invading species is essential to anticipate and potentially lessen impacts. Fisheries scientists in western Asia documented meristics, ecology, and life history characteristics of introduced northern snakehead. Their interest in northern snakehead biology developed in part because by 1970 northern snakehead were contributing to commercial fish harvests (Guseva, 1990). Growth by individuals and the population was rapid; one report documented a single seine haul capturing more than 400 kg (Amonov, 1974). To assess potential contribution to riverine and reservoir fisheries, several central Asian authors documented annual growth rates of individuals, using length-at-age data, which we compared to growth rates across the species' native range (Table 1).

Introduced fish may adapt their life history strategies, including differences in growth and reproduction (Haynes & Cashner, 1995), because they are exposed to a new biotic community and a different suite of abiotic characteristics, such as flow and temperature regimes. These factors could impact the seasonal timing and magnitude of growth, and the timing and frequency of reproduction. Overall growth rates of northern snakehead in the introduced range of Syr Dar'ya River basin are less than those for fish from its native range in the Amur River basin for the first 2 to 3 years of life, but after reaching sexual maturity they begin to match the growth rates of fish in the native range (Dukravets & Machulin, 1978). Northern snakehead spawning is associated with a range of water temperatures. In Tajikistan, northern snakehead begin spawning when water temperatures reach 18–20°C (Amanov, 1974), but a report from Kazakhstan demonstrates that spawning also occurs at temperatures of 24°C (Dukravets & Machulin, 1978). In the Amur River basin it has been suggested that northern snakehead spawn up to five times a year; however, in its introduced range in Kazakhstan, fish spawned from one to three times per year (Courtenay & Williams, 2004).

Spread of invasive species is often inevitable; however, exploration of life history strategies can provide insights into how managers might limit rates of spread or alleviate impacts. In this article, growth of northern snakehead is compared among introduced populations in the Potomac River and Uzbekistan, and native populations in Russia and China. Selected natural history features of northern snakehead in the Potomac River are also described, including: juvenile growth rates, seasonal adult growth rates and condition, and reproductive biology throughout the spawning season. Adult growth, condition, and consumption likely all decrease during the spawning season because of the time and energy burdens of guarding offspring (Gascho Landis & Lapointe, 2010). Gonadosomatic index (GSI), a measure of spawning periodicity, is expected to correlate with spawning activity (Rinchard & Kestemont, 1996); thus, a peak in GSI was expected in late spring, when females are known to begin actively spawning (Courtenay & Williams, 2004).

Materials and methods

Northern snakehead growth was examined by three different methods: (1) comparing male and female length-at-age; (2) recapturing marked fish; and, (3) capturing sibling larvae and juveniles over consecutive days. Sex-specific length-at-age data were collected primarily through electrofishing by crews from the Virginia Department of Game and Inland Fisheries (VDGIF), Maryland Department of Natural Resources, and Virginia Cooperative Fish and Wildlife Research Unit (VCFWRU). Fish given to VDGIF biologists by anglers provided additional information. From 2004 to 2007, fish were collected via boat, backpack, and tote-barge electrofishing, primarily from April to September. Total length (TL, mm) and weight (g) of each fish were measured, and otoliths were removed. Saggital otoliths were cracked and ages were estimated by counting annuli with the aid of a dissecting microscope. Counts were performed by two experienced VDGIF biologists. In cases were annuli counts differed, a third blind reading was performed and, if consensus was not reached, the otolith was not used in the analysis.

Analysis of covariance (ANCOVA) was used to estimate differences between TL-to-age relationships for male and female fish. Mean length was calculated for each year class of Potomac River fish. To compare growth rates of Potomac River fish with other populations, mean length-at-age data were used from an introduced population in Uzbekistan and two native populations in the Amur River basin, Russia, and Huanghua Lake, China (Amanov, 1974; Dukravets & Machulin, 1978; Wu et al., 1999). To characterize growth, we used von Bertalanffy growth models based on the equation: $l_t = L_\infty[1 - e^{-K(t-t_0)}]$, where l_t is length-at-time of interest, L_∞ is maximum possible length, K is the growth parameter, and t_0 is the time at which l_t equals 0 (von Bertalanffy, 1938). Growth trajectories were plotted as mean length-at-age.

A concurrent radio telemetry study allowed for recapture of adult fish to assess seasonal patterns of growth. In October 2006, 49 northern snakehead were surgically implanted with radio tags with a unique radio frequency and identification number. Length and weight of each individual was recorded at the time of tagging. Incidental recaptures of six tagged fish occurred during summer electrofishing and recaptured fish were measured (TL), weighed and released. Five tagged fish were intentionally recaptured at the end of the telemetry study in October 2007. Recaptures were thus split into two time periods: (1) spawning period, when fish were recaptured over a 6-week period (5/24/2007–7/5/2007), representing 7–8 months from the date of initial measurements (six fish); and (2) 1 year after initial measurements, which occurred several months post-spawning (five fish). Additional data came from three fish: one radio-tagged by VDGIF on April 20, 2006 and recaptured on June 27, 2007, and two radio-tagged by VCFWRU in October 2006, with one recaptured on May 6, 2008 and the other recaptured on August 6, 2009.

Larval growth data were obtained through the radio telemetry study. On August 13, 2007, a tagged fish was found guarding a school of young and on August 14, 2007, a tagged fish was discovered guarding a nest of eggs which soon hatched (Gascho Landis & Lapointe, 2010). Radio telemetry was used to locate adults guarding these two schools on most consecutive days for 2 weeks. Northern snakehead begin breathing air very young (several days old) (Courtenay & Williams, 2004), which made them vulnerable to capture. A sample of young snakehead was collected daily for 13 days (except for days 2, 3, and 11) associated with the fish first located on August 13, and for 11 days (except day 10) associated with the fish first located on August 16.

To assess GSI patterns, fish were captured by electrofishing from April through October 2007. GSI was calculated only for females, by dividing gonad weight by total fish weight. GSI was plotted against water temperature from Dogue Creek Bay. Because

Dogue Creek contained the highest population density of northern snakehead in the Potomac River (80% of the sampled population, Odenkirk & Owens, 2007), temperatures taken here provide a reasonable index of the thermal experience of most fish collected. Temperatures were recorded from April through July 2007, while electrofishing and locating radio-tagged fish. Multiple readings were recorded at the water surface throughout the bay and daily temperatures were reported as averages (2–20 readings per day). Analysis of variance (ANOVA), with post-hoc Tukey HSD tests, was used to evaluate differences in GSI among months.

Diet items were collected from all northern snakehead, stomach contents were weighed to the nearest gram, and empty stomachs were recorded. Ration size was calculated as the average meal size (g) consumed per captured fish for a given month (excluding empty stomachs). Fish condition was assessed using residual weights of fish collected in the Potomac River catchment from 2004 to 2007. Length–weight relationships, based on regression analysis of log-transformed data (Male $R^2 = 0.99$, Female $R^2 = 0.99$) were developed separately for male and female fish. Data were combined from throughout the year to create a global model. Residual weight for each individual fish was calculated from original length-weight regressions. Positive residuals indicate above-average condition and negative residuals indicate below-average condition. Mean residuals for each summer month were used to assess population-level trends in condition, and ANCOVA with Tukey HSD tests was used to assess differences in residuals among months, with length as a covariate. JMP 5.1 was used to perform statistical analysis (SAS Institute, Inc., Cary, NC; http://www.jmp.com).

Results

From the Potomac River, 173 northern snakehead were aged, and ranged from 1 to 7 years old. There was no difference in length-at-age for male and female northern snakehead ($F = 0.0618$, df = 1, $P = 0.8039$); thus, all fish were combined in the von Bertalanffy growth equation, which was $Lt = 1388[1 - e - 0.073(t - 1.32)]$. As expected, fish exhibited decreasing annual growth rate with increasing age. The von Bertalanffy growth model for length-at-age for the Uzbekistan population was $Lt = 1608[1 - e - 0.071(t - 0.99)]$, the model for the China population was $Lt = 745[1 - e - 0.39(t - 0.024)]$, and the model for the Russia basin population was $Lt = 868[1 - e - 0.237(t - 0.242)]$ (Fig. 1). The theoretical maximum length (1388 mm) for northern snakehead in the Potomac River is intermediate between the Uzbekistan and the China and Russia populations, and the growth-rate factor (K) for the introduced populations (Potomac and Uzbekistan) is an order of magnitude lower than native population.

Seasonal growth rate was assessed by measuring recaptured tagged fish ($n = 11$) (Table 2). The average increase in length and weight from October to the following spawning season was 14 (SD ± 11) mm and 182 (SD ± 85) g, respectively. The average increase in length and weight from the spawning season to the end of the year was 92 (±17) mm and 830 (SD ± 534) g, respectively. The annual growth rates observed for individual fish were similar to the average growth increment calculated from length-at-age information; the growth increment for fish between years 5 and 6 (the most likely age of many of the tagged fish) was 99 mm. The individuals tagged by VDGIF and VCFWRU recaptured 14, 18, and 34 months later, respectively, had increased 269, 142, and 119 mm (Table 2).

Larval fish growth accelerated during the first few weeks of life (Fig. 2). Although larval fish length and

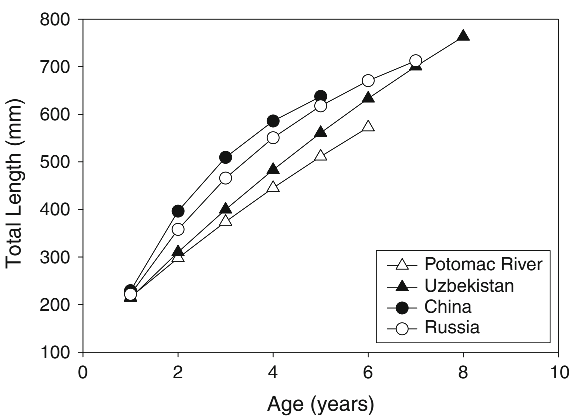

Fig. 1 Mean length-at-age relationships for northern snakehead populations introduced into the Potomac River and Uzbekistan, and from the native range in China (Huanghua Lake) and Russia (Amur River basin)

Table 2 Original weight (g) and length (mm, total length) at tagging, which occurred between October 11 and 26, 2006, and length and weight at recapture

The fish recorded at the top of the table were recaptured during the spawning season and the fish at the bottom were recaptured after 1 year

2006				2007		
Fish number	Length	Weight	Days at large	Length increase	Weight increase	Daily growth (mm/d)
Recaptured during spawning season						
533	590	1868	211	14	106	0.07
1504	569	1648	217	−5	160	0
1363	578	1732	218	12	156	0.06
1645	644	2490	226	22	340	0.09
674	445	790	238	12	124	0.05
214	602	2156	253	30	208	0.12
Recaptured after 1 year or longer						
134	604	2231	365	98	1499	0.27
171	562	N/A	365	70	N/A	0.19
654	503	1060	365	114	562	0.31
1363	578	1732	365	79	272	0.22
1723	554	1686	365	97	988	0.26
94[a]	446	886	434	269	2122	0.62
191[b]	512	654	559	142	2596	0.25
345[c]	539	658	1016	119	1250	0.18

[a] Fish 94 was tagged by VDGIF on April 20, 2006

[b] Fish 191 was tagged by VCFWRU in October 2006 and recaptured on May 6, 2008

[c] Fish 345 was tagged by VCFWRU in October 2006 and recaptured on August 6, 2009

weight did not overlap between the two nest cohorts we observed, fish length was similar between the last capture of the younger school and the first capture of the older school. This suggests the fish last captured from the younger school were a day or two younger than the fish first captured from the older school. Growth (especially weight) of young was slow over the first 2 weeks then exhibited a nearly exponential trajectory (Fig. 2). Fish TL at hatching was 3.4 mm (SD $\pm$ 0.68, $N = 9$). During what was estimated to be the third week after hatching, daily growth was 2.3 (SD $\pm$ 0.7) mm in length and 0.04 (SD $\pm$ 0.02) g in weight.

Seasonal variation in GSI reflected spawning activity. From April to October, female northern snakehead GSI ranged from 0.3 to 10.5%. Monthly GSI averages were significantly different ($F = 12.91$, df $= 7$, $p < 0.001$). Average GSI quickly increased between April and June (Fig. 3). At the peak in June, GSI levels were highly variable, indicating considerable asynchrony in female gonad development. The average and range of GSI declined from June until October, when the monthly average was lowest. Temperatures in Dogue Creek Bay also rose quickly at the end of March, until reaching a plateau in June (Fig. 3). Water temperatures averaged 26°C during peak GSI levels at the beginning of June.

Northern snakehead condition, as measured by residual weight, was greatest in May, declined during summer, then rose during fall (Fig. 4A). Although growth rate and length-at-age did not differ between sexes, conditions of the sexes were analyzed separately because of potential differences in behavior and physiology. A clear pattern of declining condition coincided with the onset of spawning. Both sexes exhibited similar seasonal patterns in condition. Monthly average female condition differed significantly during May–October ($F = 13.14$, df $= 5$, $P < 0.001$). Tukey's HSD showed that female condition was lower in June and July than in April and October. Male condition also differed significantly among months ($F = 7.57$, df $= 5$, $P < 0.001$). Tukey's HSD showed that male condition was higher in May than in July, August, September, and October.

Seasonal patterns in ration size were similar to those observed for fish condition. For fish with food in their stomach, ration size declined to low levels in July then increased by October. The number of fish without food in their stomachs increased from 49% for males and 29% for females in May to 70% for males and 58% for females in June. In July, 70% of males and 23% of females lacked food in their stomachs. However, even with this decrease in frequency of empty female stomachs, ration size remained small.

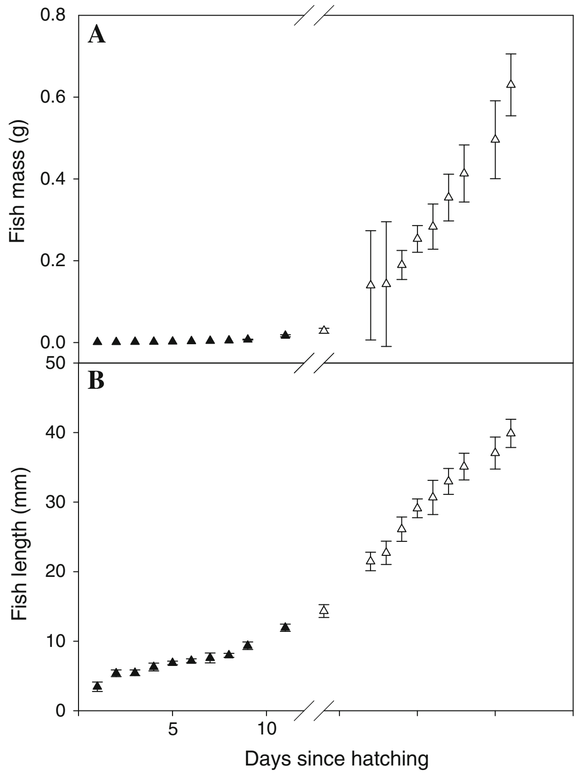

Fig. 2 Larval growth rate as measured by daily mass increase (**A**) and daily length increase (**B**) since hatching. The split in each panel distinguishes data from the school guarded by parent fish 433 (*solid triangles*) and 573 (*hollow triangles*). The hatch date for the young of fish 573 is unknown and thus no dates occur on the *x*-axis for these lengths and weights

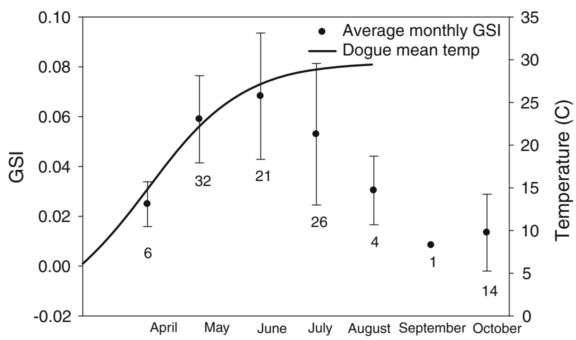

Fig. 3 Female northern snakehead GSI ($N = 104$) plotted against the month of fish collection. Error bars represent one standard deviation. The number underneath each point is the sample size of females for each month. Plotted curve represents average daily surface water temperatures in Dogue Creek Bay, Potomac River

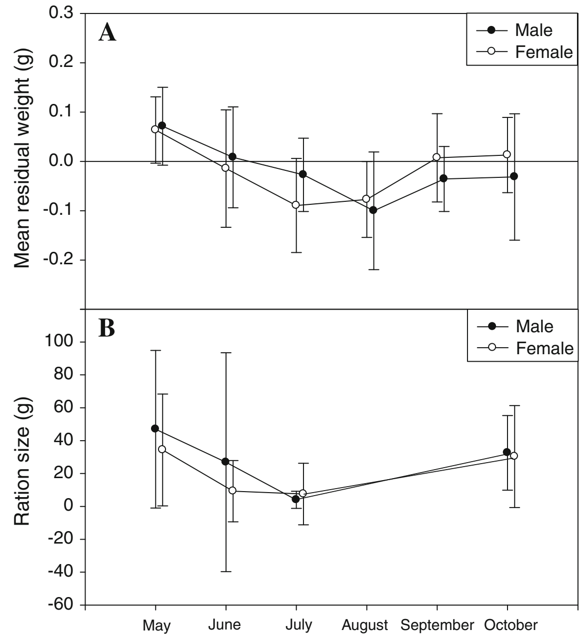

Fig. 4 Mean monthly residual weight (**A**) and ration size (**B**) for male and female northern snakehead in the Potomac River, 2007. Positive residuals indicate above-average weight and negative residuals indicate below-average growth. Error bars represent one standard deviation

Discussion

Individual growth of northern snakehead in the Potomac River catchment was slower than in native and introduced populations in Asia. Although, it is unclear what is responsible for the depressed growth of Potomac River snakehead, it may be related to energetic constraints placed by the thermal experience of the fish. In laboratory experiments, Liu & Cui (1998, 2000) found that consumption by northern snakehead was maximized at 28.6°C, and declined at higher temperatures. Subsequent experiments revealed that resting respiration rates increased substantially at 35°C, demonstrating that high temperatures physiologically stressed the fish (Liu & Cui, 2000). In addition, obligatory air-breathing increased metabolic rate by requiring fish to swim to or remain near the water surface. In July and early August, average water temperature in Dogue Creek Bay was 29.3°C, with daily temperatures often >30°C (our highest recorded temperature was 36°C). Northern snakehead growth may potentially be limited during summer months by high metabolic costs of respiration. The data from the

Russian and Chinese populations of northern snakehead examined in this study are from more northerly latitudes and experience cooler summer temperatures that are probably closer to their thermal optima. To evaluate temperature differences between the regions, we examined average July air temperatures at locations in close proximity to the four different collection sites of northern snakehead. Previous research has shown a correlation between air temperature and water temperature (Flint & Flint, 2008). Although, this relationship may not always be a 1:1 linear relationship, increases in air temperature result in corresponding increase in water temperature (Morrill et al., 2005). Average temperatures close to the Russian site are 20.5°C (Komsomol-sk-na-Amure, Russia, 50N, 137E, 20 year average), the Chinese site are 20°C (Changchun, China, 43N, 125E, 81 year average), the Uzbekistani site are 25.5°C (Aral Bay, Uzbekistan, 42N, 59E, 73 year average), and the Potomac River site are 26.1°C (Washington, DC, USA, 38N, 77E, 51 year average) (www.weatherbase.com). The ambient air temperatures at the sites of northern snakehead introduction, Uzbekistan and the Potomac River, are considerably higher than the sites in their native range. We hypothesize that the differences in temperature may limit introduced northern snakehead growth and potentially their overall success.

Although Potomac River northern snakehead growth may be reduced by metabolic cost, additional factors may contribute to the reduced growth rate. Examining seasonal patterns of consumption and condition can help identify bottlenecks in overall annual growth trajectories, as well as provide useful life history information for the Potomac River population. A key additional factor limiting growth during summer is the energetic costs of tending their young. In the Potomac River, predators of juvenile fishes are abundant (personal observation), requiring high energetic investment in parental care. For northern snakehead, average ration size plummeted and the frequency of empty stomachs increased during summer. Decreases in condition and growth have been noted for other species while guarding nests and young (Hinch & Nicholas, 1991). For example, male largemouth bass (*Micropterus salmoides*) feed very little while guarding their nest and larvae (Heidinger, 1975), leading to low growth rates during the spawning period (Adams et al., 1982).

Seasonal consumption patterns of northern snakehead show mixed agreement when compared to those documented elsewhere in the species range. In the Amu Darya River in Kazakhstan, northern snakehead began feeding in spring when water temperatures exceeded 10°C (Guseva, 1990). From late March through May, fish consumed 45% of their annual ration. This corroborates findings from the Potomac River, where large ration sizes in spring appeared to support above-average body condition and fueled gonadogenesis. However, the central Asian pattern differs in that consumption continued at a high rate in June and July, with fish consuming an additional 47% of their annual ration (Guseva, 1990). This was followed by a gradual decline in consumption during August. In contrast, consumption by Potomac River fish decreased dramatically in June and July. The timing of this decrease in consumption and condition corresponds well to the peak in spawning activity; thus we suspect a link to reproduction costs and responsibilities of nest guarding.

Most somatic growth by northern snakehead in the Potomac River occurred after the spawning season. Fish tagged in October 2006 grew little through the following year's spawning season, but had grown substantially by October 2007. Previous studies of northern snakehead have documented little growth during winter (Guseva, 1990; Liu & Cui, 1998). Although spring water temperatures were favorable for foraging, energy consumed was probably directed toward gonadal growth. The relatively high ration sizes observed prior to spawning suggest that growth was not limited by consumption. Overall, it appears that growth of the Potomac River northern snakehead population is limited during the summer months; however, caution should be used when evaluating these trends because of a low sample size. This restriction may represent an interaction between high temperatures driving increased metabolic rate and the energy costs of nest guarding.

Larval northern snakehead grow rapidly, which likely enhances survival to the juvenile stage (Houde, 1994). Courtenay & Williams (2004) reported that exogenous feeding begins at 8 mm TL. Rapid growth began as fish approached 8 mm TL, which coincides with to the onset of exogenous feeding. After initiation of exogenous feeding we observed a larval growth rate of 2.3 mm per day.

Growth patterns observed for northern snakehead have several potential implications. When compared to other populations of northern snakehead, the growth of Potomac River population is slow. By growing at a slower rate, these fish may require a lower caloric intake to match their growth potential. This growth limitation may be alleviated at higher latitudes in North America which have lower mean summer temperatures and more closely approximate conditions of their Asian distribution. Increased growth rates at higher latitudes could drive greater competition for prey resources. Physiological studies, such as actual consumption and respiration rates of Potomac River northern snakehead, and mechanistic studies, such as competition experiments, would improve our understanding of their impact on North American freshwater ecosystems. Northern snakehead have the potential to spread as far north as Hudson Bay (Herborg et al., 2007). Results suggested that northern snakehead impacts could be greater in northern areas of North America due to an increased potential for growth.

The patterns observed for GSI were consistent with existing knowledge of northern snakehead reproduction. Throughout the 2007 spawning season, GSI trends were similar to those presented by Odenkirk & Owens (2007), including a peak for GSI in the first week of June. Water temperatures during this period in 2007 averaged 26°C. Reports from central Asia indicate that northern snakehead begin spawning at water temperatures of 18–20°C (Amanov, 1974). In 2007, water temperatures in the bays of the Potomac River warmed to 18–20°C by the last week in April, which corresponded with an initial rise in GSI (Fig. 3).

GSI data indicated that northern snakehead spawn over several months in the Potomac River, which is consistent with previous studies. Courtenay & Williams (2004) reported spawning of up to five times per year in the species' native range, while in their introduced range in Kazakhstan fish spawn up to three times per year (Dukravets, 1992). Limited data on ovary development precludes distinguishing between asynchronous single spawns by individuals over several months versus multiple spawns by individuals over several months; however, synchronous patterns in GSI were not observed, suggesting that individuals spawned asynchronously.

Multiple spawning events and significant guarding of young typically do not co-occur as tactics in fish life history strategies. Multiple spawning is an "opportunistic" tactic (Winemiller & Rose, 1992) often associated with small fishes and habitats structured by stochastic events. Opportunistic species take advantage of such dynamic processes by producing small clutches of eggs multiple times. In contrast, nest guarding is an "equilibrium" tactic, in which parents produce small clutches of large eggs, which are protected by the parents (Winemiller & Rose, 1992). Although, northern snakehead do guard their young for up to 9 weeks (Ling, 1977), they also have moderately large clutches of eggs (Courtenay & Williams, 2004), which suggests an intermediate strategy that would make multiple spawns extremely costly. Nevertheless, similar to previous accounts (Dukravets & Machulin, 1978), we frequently observed spent females containing small, inchoate eggs, suggesting the fish had recently spawned and was beginning to develop new eggs. Thus, the potential for multiple spawning seems to exist, although it may be limited by the extended guarding and the toll this takes on fish condition.

Success of control efforts for northern snakehead may be limited by their reproductive flexibility. The Potomac River population will likely continue its rapid increase in abundance due to its ability to spawn throughout the summer. This may ensure continuous successful year classes because young are produced across the range of potential environmental conditions. Control efforts may be most cost-effective during summer, when fish are actively involved with reproduction; detection during this period may enable managers to eliminate parents as well as their young offspring (Jiao et al., 2009).

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