Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate

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Abstract: Invasive species often have rapid and far-reaching negative impacts on populations and ecological communities. These effects are most common when invasive species have few competitors or predators. Although higher level carnivores do consume invasive species, quantitative effects of new and abundant food sources on predators have rarely been documented and, as a consequence, potentially positive effects of invasive species may be under appreciated. We investigated the effects of the invasive round goby (*Neogobius melanostomus* (Pallas, 1814)) on diet composition, growth rate, and body size of the Lake Erie Water Snake (*Nerodia sipedon insularum* (Conant and Clay, 1937)), which is threatened in the USA and endangered in Ontario, Canada. Water Snakes have shifted their diet, and round gobies now constitute >92% of prey consumed. This shift in diet has occurred in just one or two Water Snake generations, yet has resulted in more rapid growth and attainment of larger body size in Water Snakes. These positive effects may reduce predation, speed reproductive maturity, increase offspring production, and fuel population growth of this threatened species.

Résumé : Les espèces envahissantes ont souvent des impacts immédiats et de grande portée sur les populations et les communautés écologiques. Ces effets sont plus fréquents lorsque les espèces envahissantes ont peu de compétiteurs ou de prédateurs. Bien que les carnivores de niveau supérieur consomment en fait les espèces envahissantes, on a peu étudié les effets quantitatifs de ces sources nouvelles et abondantes de nourriture sur les prédateurs et, en conséquence, on peut sous-estimer les effets potentiellement bénéfiques des espèces envahissantes. Nous avons étudié les effets de l'envahisseur, le gobie à taches noires (*Neogobius melanostomus (*Pallas, 1814)), sur la composition du régime alimentaire, le taux de croissance et la taille corporelle de la couleuvre d'eau du lac Érié (*Nerodia sipedon insularum* (Conant et Clay, 1937)), une espèce menacée aux É.-U. et en danger d'extinction à l'Ontario, Canada. Les couleuvres d'eau ont changé leur régime alimentaire et les gobies à taches noires constituent maintenant >92 % des proies qu'elles consomment. Ce changement de régime s'est produit au cours de seulement une ou deux générations des couleuvres; il en est résulté, cependant, chez les couleuvres une croissance plus rapide et une taille corporelle plus grande. Ces effets positifs peuvent réduire la prédation, accélérer la maturité reproductive, augmenter la production de petits et soutenir la croissance de la population chez cette espèce menacée.

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Introduction

Invasive species are recognised as a primary threat to biodiversity (Diamond 1984). In the North American Great Lakes, aquatic invasive species have precipitated declines in native species and resulted in a major reorganisation of aquatic food webs (Stewart et al. 1998; Ricciardi and MacIsaac 2000; Ricciardi 2001). One recent invader, the round goby (*Neogobius melanostomus* (Pallas, 1814)), arrived from the Black or Caspian Sea via ballast-water discharge in the early 1990s and spread quickly to all five Great Lakes (Marsden and Jude 1995; Jude 1997; Corkum et al. 2004). These fish feed on two other Ponto-Caspian invaders, zebra mussels (*Dreissena polymorpha* (Pallas, 1771)) and quagga mussels (*Dreissena bugensis* Andrusov, 1897) (Ray and Corkum 1997), which themselves have had dramatic ecological impacts (Stewart et al. 1998). Round gobies also feed on native macroinvertebrates and on eggs and larvae of native fishes — yellow perch (*Perca flavescens* (Mitchill, 1814)), walleye (*Sander vitreus* (Mitchill, 1818)), smallmouth bass (*Micropterus dolomieu* Lacepède, 1802), shiners (*Notropis* Rafinesque, 1818), roughbelly darters (*Percina* Haldeman, 1842) — (French and Jude 2001; Steinhart et al. 2004*a*), and compete with other native fishes — mottled sculpin (*Cottus bairdi* Girard, 1850), logperch (*Percina caprodes* (Rafinesque, 1818)) — for food and space (Janssen and Jude 2001). In Lake Erie, round gobies were first reported from the mouth of the Grand River in 1993 and the mouth of the Ashtabula River in 1995 (Marsden and Jude 1995). They are now common in the western basin of Lake Erie with an estimated population size of 9.9 billion (Johnson et al. 2005).

Lake Erie's western basin is also home to the endemic Lake Erie Water Snake (*Nerodia sipedon insularum* (Conant and Clay, 1937)), which is threatened in the USA and endangered in Ontario, Canada, and Ohio, USA (Fazio and

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Szymanski 1999). This non-venomous colubrid snake occurs only in the island region of western Lake Erie. The 18 islands range in size from 0.5 to 4260 ha and are 0.3–22.4 km from the mainland. The island region is less than 40 km in diameter, giving the Lake Erie Water Snake one of the most restricted geographic distributions of any North American vertebrate taxon. In contrast, the northern Water Snake (*Nerodia sipedon sipedon* (L., 1858)), which is found in adjacent mainland habitats, ranges across much of eastern and mid-western North American (Gibbons and Dorcus 2004; Walley et al. 2006). Lake Erie Water Snakes differ in colour pattern from northern Water Snakes (Conant and Clay 1937); a difference that is maintained by a dynamic balance between natural selection and gene flow (King 1993*b*, 1993*c*; King and Lawson 1995, 1997). Restricted geographic distribution and declining population size, attributed to human persecution and habitat loss, resulted in US federal protection in 1999 (Fazio and Szymanski 1999). Recovery efforts target these threats through public outreach, land acquisition, and habitat management (US Fish and Wildlife Service 2003).

Here, we describe a rapid and nearly complete shift in Lake Erie Water Snake diet from native fishes and amphibians to round gobies. Although alien species often have large-scale impacts (Ricciardi and MacIsaac 2000; Ricciardi 2001; O'Dowd et al. 2003; Ruiz and Carlton 2003; Mooney et al. 2004), only rarely are quantitative pre-invasion and post-invasion data available. In contrast, nearly annual population monitoring of Lake Erie Water Snakes since 1980 allows for the detailed analysis of effects of round gobies. In particular, we demonstrate increased growth rate and body size among Water Snakes following the round goby invasion. We rule out differences in weather as a possible explanation for these changes (cf. Blouin-Demers et al. 2002). Thus, in addition to providing an abundant food source, round gobies may benefit Water Snakes through increased growth rate and body size.

Methods

Water Snakes were hand-captured during area-constrained searches at study sites on Pelee, Kelleys, South Bass, Middle Bass, North Bass, Middle, and Gibraltar islands. Water Snakes were measured to obtain snout–vent length (SVL) and mass, classified by sex (Fitch 1987; King 1986), individually marked by scale clipping or passive integrated transponder (PIT) tags, and released at their site of capture. Fieldwork was conducted over four sets of consecutive years: 1980–1985, 1988–1992, 1996–1998, and 2000–2004.

Prey items were recovered when Water Snakes regurgitated voluntarily or following manual stimulation of individuals in which a food bolus was clearly evident (King 1993*a*; King et al. 1999). Quantitative data on Water Snake diet composition before and after the round goby invasion come from an unspecified number of prey recovered from 23 preserved Water Snake specimens collected on Pelee Island in 1948 (Hamilton 1951) and from prey collected throughout the island region during 1988–1992 (45 prey from 31 Water Snakes; King 1993*a*), 1996–1998 (46 prey from 45 Water Snakes; King et al. 1999), and 2003–2004 (322 prey from 299 Water Snakes; this study). Quantitative data on prey composition were not collected during 1980–1985, although prey taxa were identified when recovered (King 1986).

Growth rate was analysed from SVL measurements of snakes captured in successive years prior to (1980–1985, 1988–1992) and following (2000–2003) the round goby invasion. Growth rate was calculated as the change in SVL divided by the number of "growth days" between captures. Since snakes do not grow during hibernation (Gregory 1982), which in Lake Erie Water Snakes lasts ca. 193 days (17 October – 27 April; R.B. King and K.M. Stanford, unpublished data), days in hibernation were subtracted from the total days between captures to obtain "growth days". Analysis of covariance (ANCOVA), with mean SVL (average SVL at first and second captures) included as a covariate, was used to test for differences in growth rate between males and females before and after the round goby invasion. Annual growth increments were determined for 47 males and 54 females before the round goby invasion and for 108 males and 101 females after the round goby invasion.

To test if differences in Water Snake growth rate before and after the round goby invasion could be attributed to variation in weather, we obtained daily temperature data from the NOAA weather station in Sandusky, Ohio, ca. 15 km from the nearest island (WBAN #14846; National Climatic Data Center 2006). Most Water Snake growth intervals ran from May/June of one year to May/June of the following year, so we used mean summer temperature (computed from daily minima and maxima for May–September) of the year of initial capture as an index of weather conditions associated with a given growth interval. Because local weather conditions are sometimes a poor predictor of demographic parameters (Hallett et al. 2004), we also obtained summer (June, July, August) principle-component-based North Atlantic Oscillation (NAO) index values (Stenseth et al. 2003; Hurrell 2005). We then repeated the analysis of covariance described above with either mean summer temperature or summer NAO included as a second covariate. If variations in weather were responsible for differences in Water Snake growth rate before and after the round goby invasion, we expected a significant covariate effect of either mean summer temperature or summer NAO and a nonsignificant effect of period (pre-round-goby invasion vs. post-round-goby invasion).

Within a given year, Water Snakes are born over a period of a few weeks in late summer and early fall, and first-year snakes (less than 1 year old) appear as a distinct size class among wild-caught individuals (Figs. 3 and 4 in King 1986). First-year snakes were identified from size-frequency histograms of captures within 2–4 week periods before (1980–1985) and after (2000–2003) the round goby invasion (few first-year snakes were measured in 1988–1992 and 1996–1998, and therefore were excluded from the analysis). Sufficiently large sample sizes of first-year snakes were available for two periods (16 May – 5 June, 1 – 31 July) both before and after the round goby invasion. Mean capture date was 22 May and 2 June for pre-round-goby and post-round-goby May/June samples (n = 116 and 107, respectively) and 18 July and 13 July for pre-round-goby and post-round-goby

July samples (n = 51 and 37, respectively). Mean SVL was compared before and after the round goby invasion using Student's t tests.

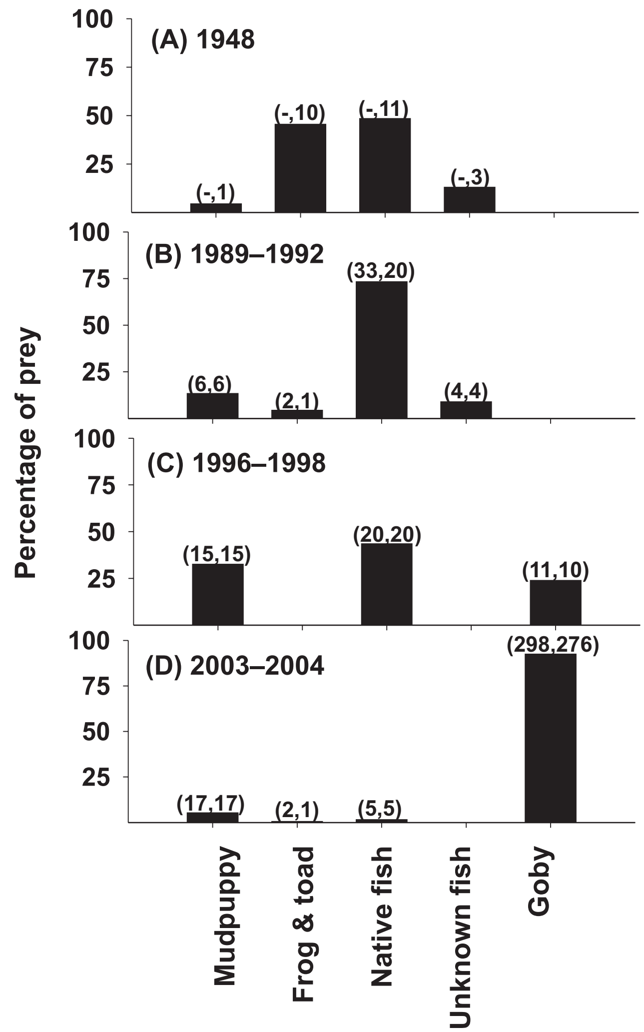
Adults were identified based on size (King 1986): males ≥430 mm and females ≥590 mm SVL. Initially, mean SVL was compared between pre-round-goby samples (1980–1985 vs. 1988–1992), between post-round-goby samples (1996–1998 vs. 2000–2003), and between pre-round-goby and post-round-goby samples (1980–1985 vs. 1996–1998, 1980–1985 vs. 2000–2003, 1988–1992 vs. 1996–1998, 1988–1992 vs. 2000–2003) separately for males and females using the distribution-free Kolmogorov–Smirnov tests with sequential Bonferroni adjustment of α for multiple tests (Ray 2004); the large sample size allowed for the inclusion of all sampling periods. These analyses revealed no differences between pre-round-goby samples or between post-round-goby samples, but consistently significant differences between pre-round-goby and post-round-goby samples (P < 0.001) (Ray 2004). Therefore, pre-round-goby samples were pooled, post-round-goby samples were pooled, and Student's t tests were used to compare mean SVL before (1980–1992; n = 668 males and 578 females) and after (1996–2003; n = 1645 males and 1470 females) the round goby invasion separately for males and females.

The Canadian Wildlife Service, Ohio Department of Natural Resources Division of Wildlife, Ontario Ministry of Natural Resources, and US Fish and Wildlife Service provided permits for this work. Protocols were approved by Institutional Animal Care and Use Committees at Northern Illinois University and Ohio State University and by the Canadian Wildlife Service.

Results

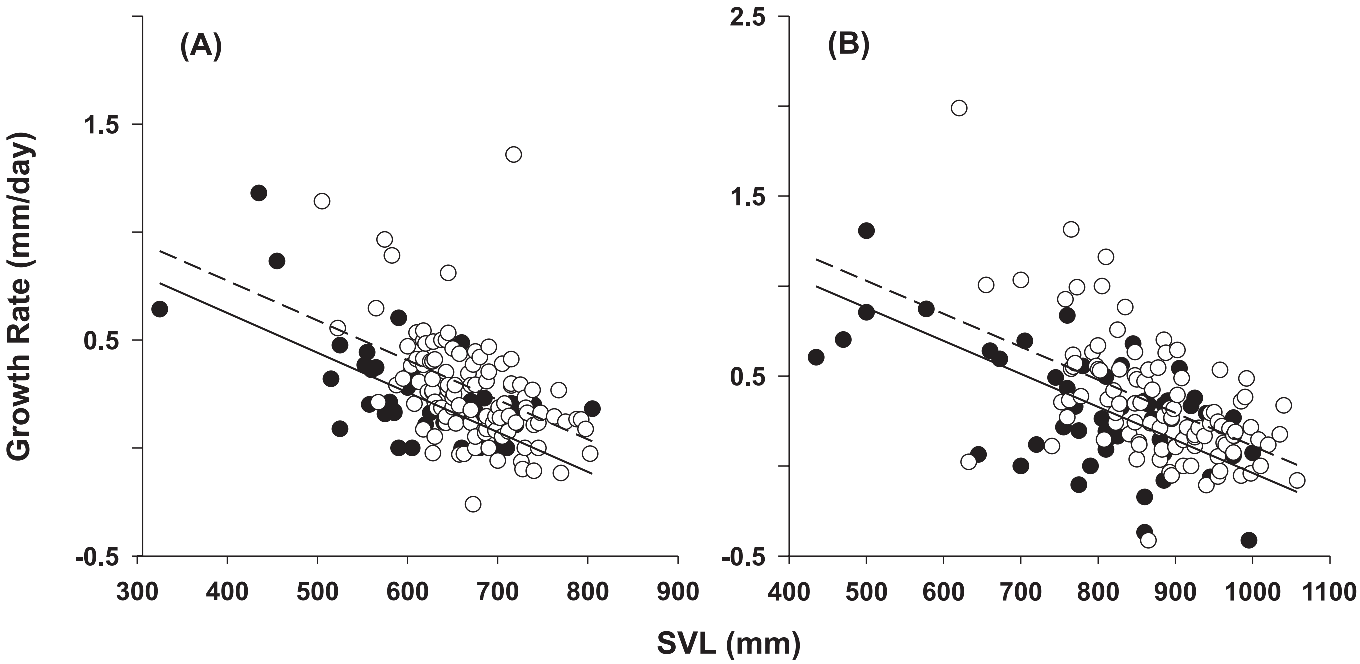
Prior to the round goby invasion, Water Snakes fed on native fishes (e.g., madtom and stonecat (*Noturus* Rafinesque, 1818), logperch (*Percina caprodes* (Rafinesque, 1818)), spottail shiners (*Notropis hudsonius* (Clinton, 1824))) and amphibians (mudpuppies (*Necturus maculosus* (Rafinesque, 1818)); Fig. 1). Round gobies appeared among Water Snake prey soon after their arrival in Lake Erie in 1995 (Charlebois et al. 1997) and constituted 24% (by number) of prey recovered in 1996–1998 samples (King et al. 1999) (Fig. 1). The proportion of round gobies among Water Snake prey has since increased and constituted more than 92% of prey recovered in 2003–2004 samples (Fig. 1). Native fishes have nearly disappeared from prey consumed by Water Snakes (less than 2% of prey recovered in 2003–2004 samples) and mudpuppies have decreased in frequency (5% of prey recovered in 2003–2004 samples compared with 14%–33% of prey in 1989–1992 and 1996–1998 samples). This diet shift has occurred in all size classes of Water Snakes; among snakes from which prey were recovered during 2003–2004, 35 were less than 1 year old, 30 were juveniles, and 178 were adults (age criteria in King 1986). Only single prey items were recovered from most Water Snakes containing prey and Water Snakes containing multiple prey items had usually consumed only a single prey taxon. Thus, prey composition was similar whether based on individual prey or individual Water Snakes (data not shown).

Fig. 1. Frequency histograms showing change in Lake Erie Water Snake (*Nerodia sipedon insularum*) diet composition before (A, B) and after (C, D) the round goby (*Neogobius melanostomus*) invasion. Data in A are based on an unspecified number of prey recovered from 23 individual Water Snakes collected on Pelee Island (Hamilton 1951). Data in B, C, and D are based on 45, 46, and 322 prey recovered from 31, 45, and 299 individual Water Snakes, respectively. Bars represent the percentage of snakes (A) or of prey (B, C, D). Numbers in parentheses above each bar show the number of prey items and the number of Water Snakes that a given prey type was recovered from (number of prey items was not reported, but multiple prey types were apparently recovered from some snakes in the 1948 sample).



There was no significant sex × period × SVL interaction effect on growth rate of Water Snakes ($F_{[3,302]}$ = 1.67, P = 0.174), indicating that the slope of the relationship between Water Snake SVL and growth rate was the same for males and females in both pre-round-goby and post-round-goby samples (Fig. 2). A significant period effect was present ($F_{[1,305]}$ = 22.85, P < 0.001), reflecting higher growth rates in post-round-goby samples. A significant sex effect was present ($F_{[1,305]}$ = 99.80, P < 0.001), reflecting higher growth rates in females. A significant covariate effect was present ($F_{[1,305]}$ = 138.59, P < 0.001), indicating that growth rates

Fig. 2. Differences in Lake Erie Water Snake growth rate for males (A) and females (B) before (solid circles, solid lines) and after (open circles, broken lines) the round goby invasion. Points represent the growth rate of individual Water Snakes captured in 2 successive years; lines represent the regression of growth rate on snout–vent length (SVL) averaged across captures. Note the differences in scale between A and B. Water Snake growth rates are significantly higher in post-round-goby samples than in pre-round-goby samples for both sexes (pre-round-goby males: growth rate = 1.36 – 0.0018SVL; post-round-goby males: growth rate = 1.51 – 0.0018SVL; pre-round-goby females: growth rate = 1.80 – 0.0018SVL; post-round-goby females: growth rate = 1.95 – 0.0018SVL).



decreased with increasing SVL. The sex × period interaction was nonsignificant ($F_{[1,305]}$ = 1.99, P < 0.159), indicating that the change in growth rate following the round goby invasion was similar for males and females. Daily growth rates were 0.44 mm/day higher following the round goby invasion (Fig. 2).

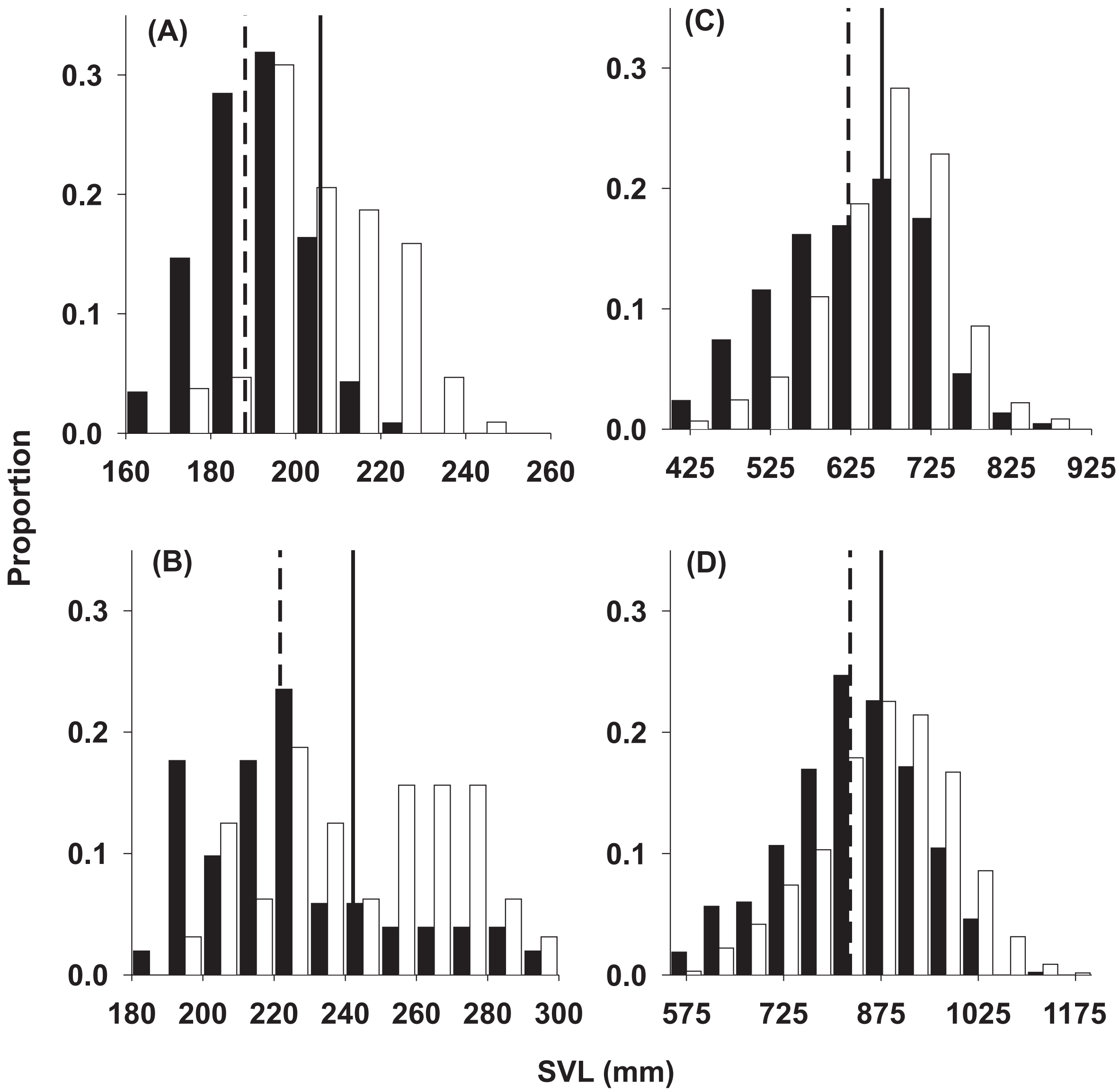
Summer temperature, weighted by number of Water Snake growth intervals, averaged 21.2 vs. 20.6 °C in pre-round-goby vs. post-round-goby years, respectively. The summer NAO index, weighted by number of Water Snake growth intervals, averaged 0.70 vs. 0.48 in pre-round-goby vs. post-round-goby years, respectively. Sample period (pre-round-goby invasion vs. post-round-goby invasion) remained significant when either summer temperature or summer NAO index was added as a second covariate in the analyses of growth rate described above (test of period effect when summer temperature was included: $F_{[1,304]}$ = 16.18, P < 0.001; test of period effect when NAO was included: $F_{[1,304]}$ = 23.75, P < 0.001). In these analyses, neither the effect of summer temperature nor the effect of summer NAO was significant (summer temperature: $F_{[1,304]}$ = 2.96, P = 0.086; summer NAO: $F_{[1,304]}$ = 1.06, P = 0.304).

Among first-year snakes captured in May/June, SVL averaged 188.1 mm in pre-round-goby samples and 205.8 mm in post-round-goby samples ($t_{[221]}$ = –10.03, P < 0.001), an increase of 9% (Fig. 3). Among first-year snakes captured in July, SVL averaged 221.7 mm in pre-round-goby samples and 242.2 mm in post-round-goby samples ($t_{[86]}$ = –3.59, P < 0.001), also an increase of 9% (Fig. 3). Among adult males, SVL averaged 622.2 mm in pre-round-goby samples and 664.0 mm in post-round-goby samples ($t_{[2311]}$ = –11.23, P < 0.001), an increase of 7% (Fig. 3). Among adult females, SVL averaged 827.4 mm in pre-round-goby samples and 875.4 mm in post-round-goby samples ($t_{[2046]}$ = –9.508, P < 0.001; Fig. 3), an increase of 6% (Fig. 3).

Discussion

Invasion of Lake Erie by round gobies has resulted in a rapid and nearly complete shift in Water Snake diet composition. Lake Erie Water Snakes reach sexual maturity in 3–4 years (King 1986) and can live for 12 or more years (snakes first marked as adults have been recaptured up to 8 years later). Thus, change in diet composition has occurred in just one or two Water Snake generations. This change is likely the result of (*i*) the super abundance of round gobies, (*ii*) declines in native prey owing to predation by and competition with round gobies, and (*iii*) differences in catchability among prey taxa. As noted earlier, round gobies reach remarkable densities in western Lake Erie (Johnson et al. 2005) and thus provide an abundant food source. Predatory and competitive effects of round gobies on native fishes are also well documented (French and Jude 2001; Janssen and Jude 2001; Steinhart et al. 2004*a*). However, evidence that this has resulted in population declines of native fishes is largely qualitative (e.g., reduced numbers observed during trawls; M. Thomas (personal communication, 2004)). Catchability also likely differs among prey types. One common foraging mode utilized by Water Snakes is to crawl along the substrate while probing in crevices among and beneath rocks and other materials (Drummond 1983; K.M. Stanford, personal observation). Strictly benthic prey (e.g.,

Fig. 3. Differences in Lake Erie Water Snake body size before (solid bars) and after (open bars) the round goby invasion among (A) first-year-class Water snakes captured in May/June, (B) first-year-class Water snakes captured in July, (C) adult males, and (D) adult females. In A–D, mean SVLs in pre-round-goby and post-round-goby samples are shown by broken and solid vertical lines, respectively. Note the differences in scale among panels. Water Snake SVL is significantly greater in post-round-goby samples than in pre-round-goby samples in all four cases.



round gobies, madtoms, stonecats, mudpuppies) may be most vulnerable to this mode of predation, whereas semibenthic prey (logperch) and prey that occur throughout the water column (spottail shiners) may be less vulnerable. Future research might profitably focus on Water Snake foraging behaviour, prey preference, and prey catchability. In addition, the impact of Water Snake predation (both in the island region and elsewhere in the Great Lakes) on round goby population dynamics may bear investigation.

Change in diet coincides with increased Water Snake growth rate. Equality of slopes of pre-round-goby and post-round-goby growth equations demonstrates that post-invasion growth is greater regardless of Water Snake size, supporting our contention that a diet shift to predominantly round gobies has occurred in all Water Snake size age classes. Furthermore, increased growth rate translates into larger body size both in first-year and adult Water Snakes.

Although changes in Lake Erie Water Snake diet composition are unequivocal, differences in Water Snake growth rate and body size following the goby invasion could potentially have other explanations. Our tests for an effect of summer temperature and summer NAO suggest that differences in weather are not responsible for changes growth rate. However, other possible explanations include (*i*) reduced intraspecific competition owing to declining snake population sizes or (*ii*) reduced human-caused mortality, especially of large individuals. Reduced intraspecific competition seems unlikely. Estimates of Water Snake density, based both on mark–recapture techniques and on the analysis of capture rate data, indicate that Water Snake population densities have remained constant or increased at 6 of 7 intensive study sites monitored between 1980 and the present (King 2003). The second possibility is that public outreach efforts aimed at reducing human-caused mortality of snakes are responsible for the patterns reported here. Capture-rate data suggest that encounters with humans most often involve adult Water Snakes (King 1986). Furthermore, adult females may be particularly vulnerable to persecution; female Water Snakes exceed males in body size (King 1986) and gravid female snakes typically exhibit increased basking behaviour and reduced locomotory capacity (Seigel et al. 1987; Gregory et al. 1999). Thus, reduced human-caused mortality could be responsible for increased adult body size, especially in females. However, reduced human-caused mortality does not provide an explanation for increased body size of first-year Water Snakes or for increased growth rate.

Increased growth rate and body size likely benefit Water Snakes in several ways. By growing quickly, Water Snakes can outgrow potential predators more rapidly (King 1993*c*) and mature sooner (as in black rat snakes (*Elaphe obsoleta* (Say in James, 1823)); Blouin-Demers et al. 2002). By growing larger, Water Snakes can produce larger litters of offspring (King 1986). Based on the relationship between female SVL and offspring number (King 1986), mean litter size is expected to have increased by 1.9 offsprings (from 21.5 to 23.4) since the round goby invasion, an increase of 9%. Given the short time since round gobies arrived in Lake Erie and their potential for rapid population growth (MacInnis and Corkum 2000), additional increases in Water Snake growth rate and body size seem possible. However, dietary shifts by other piscivore predators may limit or even reduce round goby populations (Corkum et al. 2004). Continued investigation of the impact of round gobies (e.g., on Water Snake survivorship, age and size at maturity, number and size of offspring, and foraging behaviour) would be of interest.

Longer term impacts of diet change on Lake Erie Water Snakes are unknown. Round gobies feed on zebra and quagga mussels, which because of their higher fat content accumulate contaminants to levels many times greater than those seen in native clams (Bruner et al. 1994). These contaminants are transferred to round gobies and potentially to Water Snakes, resulting in greater bioaccumulation of environmental toxins (Jude 1997). In addition, round gobies consumed by Water Snakes were smaller in maximum size (ca. 65 g) than were native prey (ca. 200 g for the largest mudpuppy consumed). This could have nutritional or energetic consequences (especially for large Water Snakes because they typically consume large prey; King 2002), as could differences in caloric content and conversion efficiencies among prey taxa. Long-term trends in round goby population size are unknown; however, given the negative impacts of round gobies on native fishes (Janssen and Jude 2001; French and Jude 2001; Steinhart et al. 2004*a*), alternative Water Snake prey may be scarce should round goby populations suddenly decrease. This could be exacerbated if the current high density of round gobies is fuelling Water Snake population growth. More complex food-web-level effects (e.g., involving round gobies, Water Snakes, and mudpuppies, which also may consume round gobies) are possible (e.g., Moore et al. 2004), as well as evolutionary changes in predators and prey (e.g., Phillips and Shine 2004).

There are a number of examples of predators that now consume introduced prey species (Adams and Mitchell 1995; Penchaszadeh et al. 2000; Harding 2003; Flueck 2004; Gregory and Isaac 2004; Kelly and Dick 2005; Maerz et al. 2005), but we know of just one other case for which quantitative data are available before and after introduction of an alien species and for which such a complete shift in diet composition has occurred so rapidly. Like Water Snakes, juvenile smallmouth bass in Lake Erie have undergone rapid diet change and accelerated growth, as well as an earlier transition to piscivory, following the round goby invasion (Steinhart et al. 2004*b*).

Although the effects of invasive species generally, and round gobies in particular, can be devastating (Janssen and Jude 2001; Ricciardi and MacIsaac 2000; French and Jude 2001; Ricciardi 2001; O'Dowd et al. 2003; Ruiz and Carlton 2003; Mooney et al. 2004; Steinhart et al. 2004*a*), increased Water Snake growth rate and body size resulting from a diet shift to predominantly round gobies, coupled with public outreach efforts aimed at reducing persecution and incidental human-caused mortality (US Fish and Wildlife Service 2003), may contribute to population recovery of this federally listed species. Such positive effects are rarely associated with invasive species (Slobodkin 2001).

Acknowledgements

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