

REVIEW PAPER

**Twenty years of invasion: a review of round goby
Neogobius melanostomus biology, spread and ecological
implications**

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The round goby *Neogobius melanostomus* is one of the most wide-ranging invasive fish on earth, with substantial introduced populations within the Laurentian Great Lakes watershed, the Baltic Sea and several major European rivers. Rapid expansion and deleterious ecosystem effects have motivated extensive research on this species; here this research is synthesized. Maps of the global distribution are provided and the invasion history of *N. melanostomus*, which spread more rapidly at first in North America, but has undergone substantial expansion over the past decade in the Baltic Sea, is summarized. Meta-analyses comparing their size at age, diet, competitors and predators in North American and European ecosystems are provided. Size at age is region specific, with saline habitats typically supporting larger and faster growing individuals than fresh water. *Neogobius melanostomus* prey differs substantially between regions, demonstrating a capacity to adapt to locally abundant food sources. *Neogobius melanostomus* comprise at least 50% of the diet of eight taxa in at least one site or life stage; in total, 16 predator taxa are documented from the Laurentian Great Lakes v. five from Eurasia. Invasive *N. melanostomus* are the only common forage fish to heavily exploit mussels in the Laurentian Great Lakes and the Baltic Sea, facilitating the transfer of energy from mussels to higher trophic levels in both systems. *Neogobius melanostomus* morphology, life history, reproduction, habitat preferences, environmental tolerances, parasites, environmental effects, sampling strategies and management are also discussed. *Neogobius melanostomus* inhabit a wide range of temperate freshwater and brackish-water ecosystems and will probably continue to spread via ballast water, accidental bait release and natural dispersal worldwide. Climate change will probably enhance *N. melanostomus* expansion by elevating water temperatures closer to its energetic optimum of 26° C. Future research needs are presented; most pressing are evaluating the economic effects of *N. melanostomus* invasion, determining long-term population level effects of egg predation on game-fish recruitment and comparing several variables (density, ecological effects morphology and life history) among invaded ecosystems. This review provides a central reference as researchers continue studying *N. melanostomus*, often as examples for advancing basic ecology and invasion biology.

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TAXONOMY

Neogobius melanostomus (Pallas 1814) is a member of the Gobiidae, one of the world's most diverse fish families, and was first described by Pallas (1814) from the Black Sea. Two sub-species are recognized from the species' native range: *Neogobius melanostomus melanostomus* (Black Sea) and *Neogobius melanostomus affinis* (Caspian Sea) (Berg, 1965). *Neogobius m. melanostomus* is the sub-species found in North America and in most non-native Eurasian populations (Baltic Sea, Danube and Dnieper Rivers); the upper Volga River population is a mix of *N. m. melanostomus* and *N. m. affinis* (Brown & Stepien, 2008). Round gobies were previously moved from the genus *Neogobius* to the genus *Apollonia* (Stepien & Tumeo, 2006), but recent phylogenetic work indicates that *Neogobius* is indeed the correct genus (Neilson & Stepien, 2009). The reclassified *Neogobius* genus is in the sub-family Benthophilinae and includes four species: *N. melanostomus*, Caspian goby *Neogobius caspius* (Eichwald 1831), monkey goby *Neogobius fluviatilis* (Pallas 1814) and Caspian monkey goby *Neogobius pallasii* (formerly sub-species *N. fluviatilis pallasii*) (Berg 1916) (Neilson & Stepien, 2009, 2011).

DESCRIPTION

The quantitative data presented in this section are from the native range based on Berg (1965) and Miller (1986) and from 48 specimens from Lake Michigan [University of Wisconsin Zoological Museum (UWZM), lots 11 046, 11 664] (N. Delventhal & J. Lyons, pers. comm.).

MORPHOLOGY

Neogobius melanostomus has an elongate body, round in cross section, with a terminal mouth, thick lips and a slightly notched tongue. The posterior angle of the jaws extends to below the anterior quarter of the eye. Body depth goes into standard length (L_S) on average 4.3 times (range 3.5–5.2) while head length goes into L_S 3.0–3.6 times. Head depth goes into head width 0.9–1.2 times. Interorbital distance is 0.8–0.9 times the eye diameter, whereas snout length is 1.1–1.4 times the eye diameter. Caudal peduncle depth is about two thirds caudal peduncle length. First dorsal-fin height goes into L_S 5.6–7.5 times, pectoral-fin length goes into L_S 3.5–4.3 times and pelvic-fin disk length goes into L_S 4.2–5.3 times.

Sexual dimorphism is marked in *N. melanostomus*: males have a larger size at age, enlarged cheeks and darker colouration. Both sexes have an erectile urogenital papilla between the anus and the base of the anal fin. The female papilla is broad and blunt (0.3–0.5 mm wide, 0.2–0.4 mm long), whereas the male papilla is longer (0.3–0.6 mm), pointed and has a terminal slit (Fig. 1).

Meristics

Neogobius melanostomus has two clearly separated dorsal fins. In its native range, the first dorsal usually has seven to eight spines and the second has one spine and 12–17 rays. Among 48 specimens from Lake Michigan, however, the first dorsal typically had only six spines (47 specimens with six spines and one with five) and the

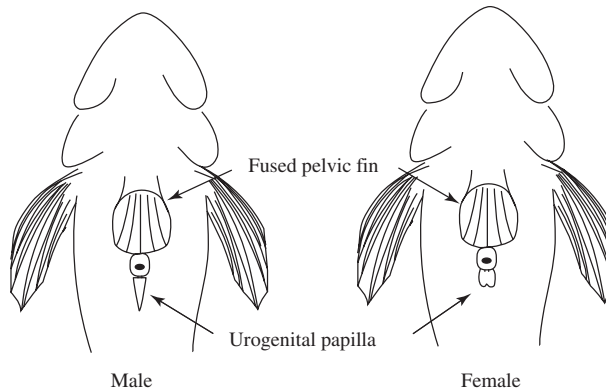


FIG. 1. Ventral diagram of male and female *Neogobius melanostomus* highlighting sex-specific urogenital papillae. Male papilla is elongate while female papilla is short and wide. Used with permission (Charlebois *et al.*, 1997).

second dorsal had one spine and 15–17 rays. The anal fin has one spine and 9–14 rays in the native range, and one spine and 11–15 rays in the 48 introduced range specimens. Two pelvic fins are united to form a suction disc, extending almost to the anus, with 17–20 total rays. There are 31–34 vertebrae and 42–59 scales in the lateral series. The lateral line comprises abundant superficial neuromasts, unlike other Great Lakes fishes, whose neuromasts are enclosed in a lateral-line canal (Jude *et al.*, 1995). The back, neck, belly, flank and a portion of the operculum are covered by ctenoid scales (Charlebois *et al.*, 1997). The nape and the top of the head are reportedly covered by cycloid scales (Stráňai & Andreji, 2004), although ctenoid scales were found from both the nape and the top of the head (M. S. Kornis, pers. obs.). Two pairs of pharyngeal tooth plates adjoin the dorsal and ventral portions of the first two branchial arches (four total plates) and are covered with disorganized incisors (Ghedotti *et al.*, 1995; L. Garrison, pers. comm.).

Pigmentation

Neogobius melanostomus exhibit variable pigmentation with grey, brown or yellow–green bodies and large dark brown lateral spots. The head is usually darker than the rest of the body. Fins are generally dark grey, although a large oblong black spot is present on the posterior portion of the first dorsal fin, starting on the fifth ray. In breeding males, the body and fins may be almost completely black, with pectoral fins sometimes fringed with white or yellow (although body colour fades to tan when the breeding male is removed from other fish).

INVASION HISTORY

MECHANISMS OF SPREAD

Evidence strongly suggests that *N. melanostomus* was transported to the Laurentian Great Lakes and the Baltic Sea *via* ballast water from transoceanic vessels. *Neogobius melanostomus* larvae are nocturnally pelagic, feeding on zooplankton at or near

the water surface (0–9 m depth) (Hensler & Jude, 2007; Hayden & Miner, 2009). Nocturnal ballasting could easily result in the transport of thousands of juveniles at a time, and night-time foraging suggests that *N. melanostomus* would be able to survive in dark ballast tanks for extended periods (Hayden & Miner, 2009). Genetic analysis points to the southern Dnieper River at Kerson, Ukraine, a major Black Sea port with frequent ballast exchange, as the primary source population for *N. melanostomus* in North America (Brown & Stepien, 2009). Ships from the Black Sea also probably introduced *N. melanostomus* to the Baltic Sea (Sapota & Skóra, 2005; Brown & Stepien, 2008).

Following its initial introduction, *N. melanostomus* has spread both through natural dispersal and through commercial shipping within invaded ecosystems. They are typically sedentary (Björklund & Almqvist, 2010) with limited home ranges [conservatively estimated at $5 \pm 1.2 \text{ m}^2$ by Ray & Corkum (2001)], but individuals occasionally move long distances. In a tagging experiment, 18 of 19 recaptured fish were caught within 67 m of the tagging site, but one fish was caught 218 days after tagging 2 km from the tagging site (Wolfe & Marsden, 1998). River colonization appears to be driven by ‘stratified dispersal’, a combination of diffusion over short distances by most individuals and long-distance colonization by migrant individuals (Bronnenhuber *et al.*, 2011). Bronnenhuber *et al.* (2011) estimated that 1.9% of individuals collected from lake sites and 7.3% collected from river sites had genotypes excluded from the population of *N. melanostomus* at a given site, and interpreted these figures to represent individuals that were first-generation migrants. A relatively high proportion of migrants in streams probably facilitates fast spread rates, with estimates ranging from 500 m year^{-1} on average (Bronnenhuber *et al.*, 2011) to up to $1\text{--}4 \text{ km year}^{-1}$ in select areas [based on upstream migration data from Kornis & Vander Zanden (2010) in tributaries to Green Bay, Lake Michigan and Green Bay trawl catch data; T. Paoli, pers. comm.]. One study in the Trent River found that *N. melanostomus* at newly invaded sites had a wider distribution of sizes and a larger mean size than at source sites (Gutowsky & Fox, 2011). Evidence of high intraspecific competition between *N. melanostomus* at high densities in streams suggests that density-dependent factors probably contribute to range expansion (M. S. Kornis, unpubl. data). Nonetheless, genetic evidence from 12 sub-populations in Lake Michigan suggests that in-lake dispersal was greatly aided by commercial shipping within the Great Lakes system (LaRue *et al.*, 2011). These findings indicate ballast water treatment and management may help limit spread of introduced species in systems like the Great Lakes and the Baltic Sea after its initial introduction (LaRue *et al.*, 2011).

North America

Neogobius melanostomus was first discovered in North America in 1990 in the St Clair River, which connects Lakes Huron and Erie (Jude *et al.*, 1992). They have since spread throughout the Laurentian Great Lakes at a faster rate than any previous fish invader (Charlebois *et al.*, 2001; Dillon & Stepien, 2001), although abundance varies between each lake (Fig. 2). At one extreme, Lake Superior, *N. melanostomus* are limited to a few harbours and tributaries. Many Laurentian Great Lakes invaders are limited in Lake Superior due to reduced disturbance, a mismatch of physiochemical characteristics with native habitats and other factors (Grigorovich *et al.*, 2003). At the other extreme, the central basin of Lake Erie, *N. melanostomus* reached an

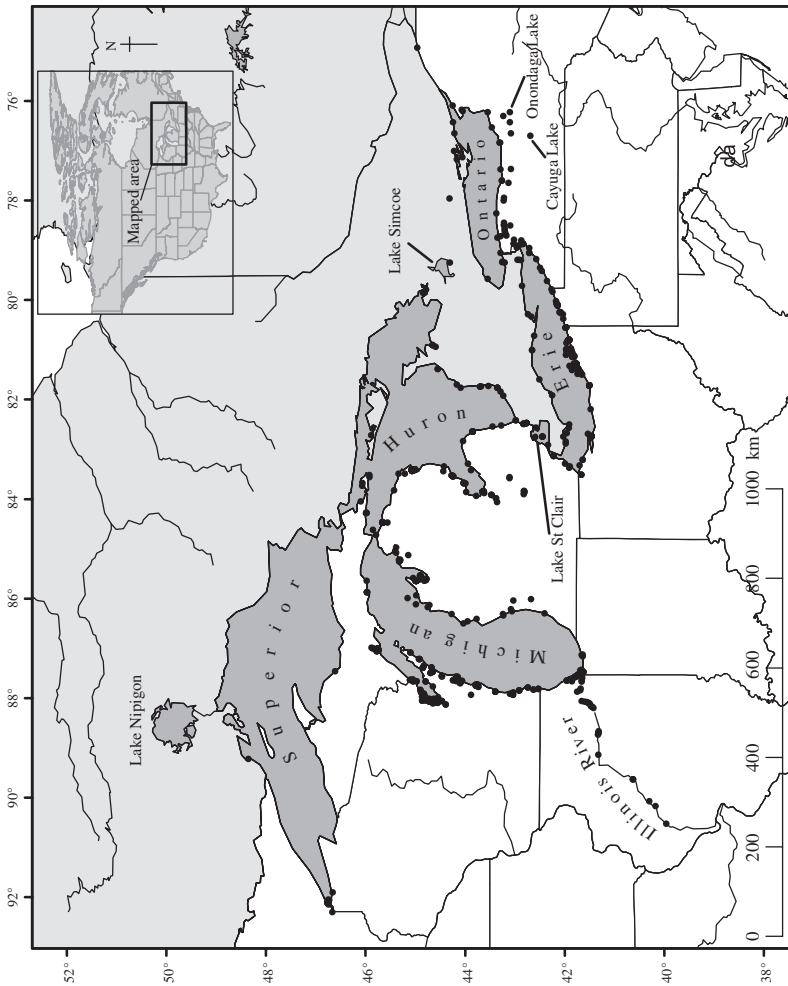


FIG. 2. Distribution of *Neogobius melanostomus* in North America, including (●) capture sites and reports confirmed by the U.S. Geological Survey (USGS). *Neogobius melanostomus* was first recorded in North America in Lake St. Clair in 1990 (Jude *et al.*, 1992). Most of the presented data are from the U.S. Geological Survey USGS Nonindigenous Aquatic Species Database. Data from Wisconsin tributaries are from Kornis & Vander Zanden (2010). Data from Ontario tributaries are from Poos *et al.* (2010) and A. J. Dextrase, J. Barnucz & the Ontario Federation of Anglers and Hunters (unpubl. data). □, Canada; □, United States.

estimated peak population size of $4.2 \times 10^9 \pm 1.5 \times 10^9$ ($\pm 95\%$ C.I.) individuals in 1999 (2789 individuals ha^{-1}) before declining to a mean of $2.2 \times 10^9 \pm 1.0 \times 10^9$ ($\pm 95\%$ C.I.) (1461 individuals ha^{-1}) from 2000 to 2002 (Johnson *et al.*, 2005a). Laboratory experiments indicate limited behavioural interactions among *N. melanostomus*, with only a 3% difference in body size needed to predict the victories in territory disputes (Stammler & Corkum, 2005). The ability to perceive size differences between themselves and other gobiids, resulting in limited aggressive interactions, could facilitate observed high densities in the Great Lakes (Stammler & Corkum, 2005). Declines in *N. melanostomus* abundance have been observed over the past 5–10 years at several other Great Lakes locations (Roseman & Riley, 2009; Young *et al.*, 2010), suggesting populations may have reached equilibrium after an initial phase of rapid growth. Although no brackish-water populations are known in North America, several studies predict that *N. melanostomus* will spread to North American coastal salt marshes and estuaries, where salinities are similar to Eurasian habitats and *Mytilus* spp. mussels could provide an abundant food source (Stepien *et al.*, 2005; Stepien & Tumeo, 2006).

Substantial genetic variation, multiple founding sources and a large number of propagules probably facilitated the success of *N. melanostomus* in North America. Almost all alleles from the primary source population were found in North American *N. melanostomus*, suggesting high propagule pressure (Brown & Stepien, 2009). Additional source populations (including the Dniester and Southern Bug Rivers, also tributaries to the Black Sea) probably contributed to North America's *N. melanostomus* population, evidenced by high genetic diversity and significant divergence across the introduced range (Brown & Stepien, 2009). Notably, populations from Saginaw Bay (Lake Huron) and several sites in Lake Ontario had unique alleles, suggesting separate introductions at those locations. Post-invasion genetic divergence in the introduced range also suggests rapid adaptation to local habitats (Brown & Stepien, 2009).

Neogobius melanostomus has spread inland from the Laurentian Great Lakes to tributary, marsh and estuary habitats. It is limited to lakes and the lowest reaches of large, slow flowing rivers in their native range and has been slow to invade flowing waters in Eurasia (Harka & B  r  , 2007). Despite this, *N. melanostomus* has established substantial tributary populations in Wisconsin (Kornis & Vander Zanden, 2010), Ontario (Poos *et al.*, 2010) and probably throughout the Laurentian Great Lakes catchment. Many of these systems contain highly diverse communities of native species, challenging the initial belief that *N. melanostomus* would be most successful in systems lacking a diverse benthic assemblage (Carman *et al.*, 2006). It has also infiltrated the Mississippi River basin (Irons *et al.*, 2006), bypassing the Chicago Sanitary Channel electric barrier prior to its activation, and has been reported in the Illinois River as far as 375 river km from Lake Michigan (A. Benson, pers. comm.). Expansion to smaller lakes and rivers adjacent to the Great Lakes is probably in an early stage: only 20% of sites predicted to be invaded by *N. melanostomus* were occupied in Wisconsin tributaries to Lake Michigan (280 of 1369 km, Kornis & Vander Zanden, 2010). Dams may ultimately limit inland range expansion, although humans have helped the species bypass dams *via* accidental introduction in several inland lakes and rivers, including Lake Simcoe and the Trent–Severn waterway in Ontario (Borwick & Brownson, 2006), Rice Lake in Ontario (J. Borwick, pers. comm.) and the Flint and Shiawassee Rivers in Michigan (D. Jude & J. Janssen,

unpubl. data). Bait-bucket transfer (due to anglers or bait store operators who capture their own bait and fail to identify and remove *N. melanostomus*) is the presumptive mechanism of dispersal upstream of dams.

Marshes were thought to be resistant to invasion due to muddy substrata and vegetation (Cooper *et al.*, 2007), but a recent study indicates that muddy habitat will support low densities of *N. melanostomus* (Young *et al.*, 2010) and in some cases density does not differ between mud and rock habitats (Taraborelli *et al.*, 2009). It has invaded the estuary of Old Woman Creek (Lake Erie, Ohio shore), one of the few protected freshwater estuaries in the nation (Brammel *et al.*, 2009) and Cootes Paradise Marsh (Hamilton Harbour, Lake Ontario), a large wetland and important breeding ground for native fishes in Lake Ontario (Young *et al.*, 2010), although low abundances in marshland habitat may limit effects on these ecosystems.

Eurasia and the Baltic Sea

Neogobius melanostomus has established numerous introduced populations in Eurasia, most notably in the Baltic Sea (Fig. 3). They were first discovered in the Baltic Sea at Puck Bay (Gulf of Gdansk) in 1990 and were probably introduced *via* ballast water of ships travelling through canals connecting the Black and Caspian Seas to the Baltic (Sapota & Skóra, 2005). Initially, spread rates were much slower than in the Great Lakes (Sapota & Skóra, 2005; Almqvist, 2008), however, *N. melanostomus* has rapidly expanded its range over the past decade and has reached high enough densities in some areas to have deleterious effects on native fish species (Karlson *et al.*, 2007) and become targets of commercial fishermen (Sapota & Skóra, 2005). Relatively new populations have been found in the western Baltic Sea along the coast of Germany (Sapota, 2004) and the eastern Baltic Sea along the coasts of Latvia and Estonia [Gulfs of Riga and Finland; Ojaveer (2006)]. It has also been captured along the southern coasts of Sweden and Finland (Björklund & Almqvist, 2010), in the Lek River, Netherlands (van Beek, 2006), in the Orda Estuary in the west Baltic (Czugala & Woźniczka, 2010), and in the Scheldt River and Albert Canal in Belgium (Verreycken *et al.*, 2011).

As in the Laurentian Great Lakes, the *N. melanostomus* invasion of the Baltic Sea is characterized by multiple introduction events and rapid adaption to local habitats. Rapid spread during the 2000s and discontinuous populations within the Baltic Sea suggest multiple introduction events (Björklund & Almqvist, 2010). Genetic analysis of six newly established populations in the southern Baltic Sea points to Puck Bay as the probable source population for other sites in the Gulf of Gdansk (Björklund & Almqvist, 2010). Despite close proximity to one another (five of six sites were within 30 km of each other), 10 of 15 genetic comparisons between these sites were significantly different, indicating rapid, site-specific genetic differentiation after only 10 generations. This evidence suggests that *N. melanostomus* rapidly adapt to new habitats, which may have contributed to its success in the Baltic Sea (Björklund & Almqvist, 2010) and the Great Lakes (Brown & Stepien, 2009).

Neogobius melanostomus [as well as several other Ponto-Caspian gobiid species, including tubenose goby *Proterorhinus marmoratus* (Pallas 1814), *N. fluviatilis*, big-head goby *Ponticola kessleri* (Günther 1861) and racer goby *Babka gymnotrachelus* (Kessler 1857)] have also spread through several major European river systems over the past two decades (Harka & Bíró, 2007). Spread in river systems is probably related to human activities such as river regulation, the connection of contiguous

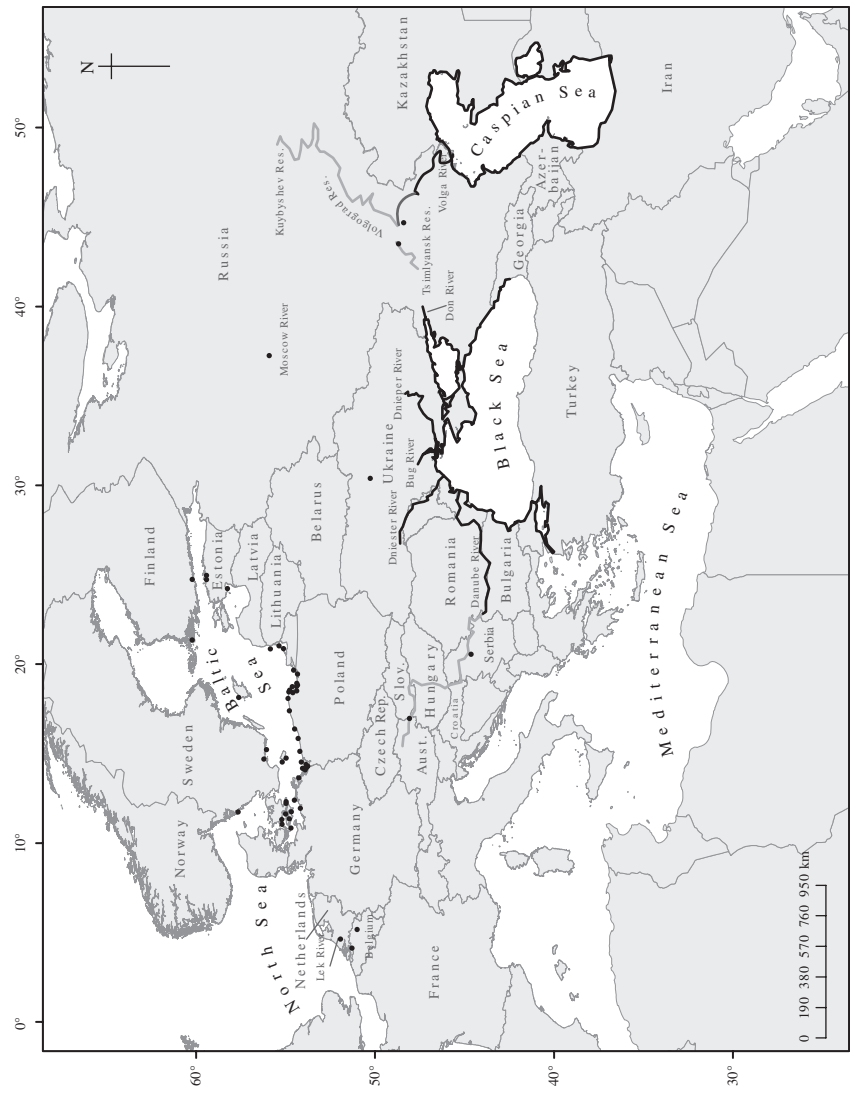


FIG. 3. Legend on next page.

basins by canals and ballast water transport by ships (Copp *et al.*, 2005). Rivers invaded by *N. melanostomus* include the Vistula River (Sapota, 2004), the Dnieper, Dniester and Don Rivers (Smirnov, 1986), the Moscow River (Sokolov *et al.*, 1989) and the Danube River through Croatia, Serbia, Hungary and Austria (Simonović *et al.*, 2001; Erös *et al.*, 2005).

REPRODUCTION

Neogobius melanostomus are multiple spawners, typically spawning every 3–4 weeks from April through to September in its native range (Charlebois *et al.*, 1997). Spawning is cued by water temperature (9–26° C), however, and both gravid females and breeding-coloured males have been captured as late as November in the Detroit River (MacInnis & Corkum, 2000a) due to prolonged warm water temperatures. Males mature at age 3 or 4 years and females at age 2 or 3 years in its native range (Miller, 1986), but both sexes may mature up to a year earlier in the Great Lakes based on findings from the upper Detroit River (MacInnis & Corkum, 2000a). Males guard nests and may not feed during spawning, suggesting most males die after one spawning season (Charlebois *et al.*, 1997), although this has yet to be confirmed. Up to 10 000 eggs from four to six females may be present in a nest, and fertilization and hatching rates are as high as 95% (Charlebois *et al.*, 1997). Eggs and larvae are relatively large (3.2 mm diameter) compared to other gobiid species (Fig. 4); as a result, a single female produces relatively few eggs (328–5221 in native range) (Kovtun, 1978). Fecundity was lower in the Detroit River than in the native range (mean 198 eggs per female with a positive linear relationship between number of eggs and L_S), but greater than most native competitor species (MacInnis & Corkum, 2000a). *Neogobius melanostomus* hatch at *c.* 5 mm total length (L_T), with black eyes, flexed urostyle and well-developed fins and digestive system; the characteristic black spot on the posterior of the spinous dorsal fin is also visible at hatching (Leslie & Timmins, 2004).

Spawning behaviour was recently observed and described in a laboratory setting, providing a detailed picture of the spawning cycle. Prior to spawning, the male excavates a nest underneath an overhanging hard substratum and fans the nest with his fins up to 10 days before egg deposition (Meunier *et al.*, 2009). During this

FIG. 3. Distribution of *Neogobius melanostomus* in Eurasia, including records of captured *N. melanostomus* outside its native range (●), rivers reported as invaded from the literature (—) and the native range as defined by Berg (1965) and Miller (1986) (—). The Kuybyshev, Tsimlyansk and Volgograd Reservoirs were invaded in the late 1960s to early 1970s (Tsyplakov, 1974; Gavlena, 1977). *Neogobius melanostomus* was found in the Moscow River in the late 1980s (Sokolov & Tsepkin, 1992). *Neogobius melanostomus* was native in the Danube River up to Vidin, Bulgaria (Smirnov, 1986), but was frequently reported in the upper Danube River beginning in the late 1990s, doubling its upstream distribution (Simonović *et al.*, 2001; Stráňai & Andreji, 2004; Erös *et al.*, 2005; Jurajda *et al.*, 2005; Harka & Bíró, 2007). The species was first recorded in the Baltic Sea in the Gulf of Gdansk, Poland, in 1990 and has greatly expanded its range since that time. Data on *N. melanostomus* in the Baltic Sea were provided by Sapota (2004), Corkum *et al.* (2004), Sapota & Skóra (2005), Ojaveer (2006), Winkler (2006), Czugała & Woźniczka (2010) and K. E. Skóra (unpubl. data). *Neogobius melanostomus* was first found in the North Sea basin in the Lek River, Netherlands, in 2004 (van Beek, 2006) and have since been reported from the River Scheldt and the Albert Canal in Belgium (Verreycken *et al.*, 2011).

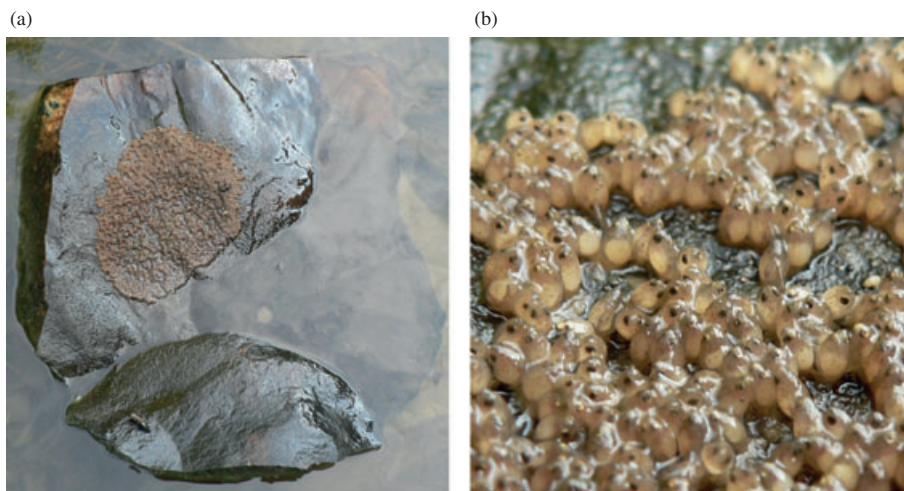


FIG. 4. Photographs of (a) a *Neogobius melanostomus* nest and (b) of *N. melanostomus* eggs. The rock in (a) has been overturned to illustrate the size and shape of a typical egg cluster. Eggs in (b) are *c.* 2 mm wide by 4 mm long and are close to hatching, as larvae have developed eyes and some larvae hatched upon handling. This particular nest was being guarded by a male *N. melanostomus*, confirming the species of these eggs.

pre-egg period, the male rubs secretions along the ceiling of the nest and may prevent females from entry. During spawning, the female and male repeatedly invert themselves to lay eggs or spread sperm on the nest ceiling; female inversions are more frequent and longer lasting and often multiple females spawn sequentially in the same nest (Meunier *et al.*, 2009). After spawning, eggs are regularly inspected by the male and are constantly ventilated by sweeping motions of the male's caudal and pectoral fins (Meunier *et al.*, 2009). The male guards the nest until the eggs hatch and exhibits three stages of aggressive behaviour when challenged by an intruder: raising pectoral and dorsal fins, emitting vocalizations and chasing and attacking the intruder (Meunier *et al.*, 2009). In the wild, *N. melanostomus* will occasionally chase potential predators, including rock bass *Ambloplites rupestris* (Rafinesque 1817) and smallmouth bass *Micropterus dolomieu* (Lacépède 1802), in addition to other gobiids (Wickett & Corkum, 1998). *Neogobius melanostomus* has been observed to sneak into nests and cannibalize eggs (Meunier *et al.* 2009), are attracted to conspecific egg odours and are able to distinguish conspecific and heterospecific egg odours *via* olfaction (Yavno & Corkum, 2011).

Visual, auditory and olfactory cues facilitate attraction between males and females, although visual cues may be predominant. In laboratory experiments, both male and female *N. melanostomus* respond to male vocalizations played through a speaker, suggesting audible cues (Rollo *et al.*, 2007). In a separate laboratory experiment, reproductive females spent significantly more time near the source of male odour compared to non-reproductive male odour and plain water (Corkum *et al.*, 2006). Electro-olfactogram (EOG) responses indicated that reproductive females had a high response to reproductive male odour, suggesting the existence of a male sex pheromone, which further study revealed as primarily excreted through urine (Corkum *et al.*, 2006; Kereliuk, 2009). A pheromonal spawning cue was confirmed

by experiments illustrating elevated EOG responses in non-reproductive females to putative steroidal pheromones extracted from reproductive males (Laframboise *et al.*, 2011). Sex pheromones may be useful in invasion-control methods, but experimentation with synthesized steroids derived from reproductive males has thus far been unsuccessful at attracting reproductive females (Corkum *et al.*, 2008). Additionally, visual cues appear to supersede pheromonal cues: a recent laboratory experiment testing both cues found that only visual stimuli (black-coloured models of males) had a significant effect on female attraction (Yavno & Corkum, 2010). This suggests that conspicuous male colouration is favoured by females, as in several other species.

Small sexually mature males with mottled colouration have been observed in several populations and probably exhibit a sneaker spawning strategy. Relative to body size, sneaker males have significantly larger testes and generate more sperm than large, black (parental) males, which have a greater investment in accessory glands and 11-ketotestosterone (Marentette *et al.*, 2009). Marentette *et al.* (2009) predicted that the ratio of parental to sneaker males would be a function of the invasion stage. Parental males would be favoured in newly colonized areas where male–male competition should be low due to an abundance of available nest sites. As the population grows, nest sites may become a limiting factor and male–male competition would increase, favouring alternative male tactics (*i.e.* sneaker spawning). Although the existence of small, light-coloured, reproductively active males strongly suggest a sneaker strategy in *N. melanostomus*, confirmation by observation of the behaviour is lacking. Hence, it is not known if sneaker males mimic females or rely on stealth and speed to spawn (Marentette *et al.*, 2009).

Neogobius melanostomus sex ratios appear to differ between introduced and native-range populations. In introduced populations, *N. melanostomus* are typically male-biased [but not always; Bergstrom *et al.* (2008)], with an operational sex ratio (sexually mature individuals) of six males to one female in the Great Lakes and three males to one female in the Gulf of Gdansk, Baltic Sea (Corkum *et al.*, 2004). More recent studies report a reduced male bias of two males to one female in both Lake Erie (Johnson *et al.*, 2005a) and Hamilton Harbour, Lake Ontario (Young *et al.*, 2010). Johnson *et al.* (2005a), however, note the overall sex ratio (all individuals) is 0.92 males to 1.00 female. Bias in operational sex ratio may be due to males remaining on the nest in a shallow habitat throughout the season while females return to deeper water to avoid predation after spawning (Kovtun, 1980). Males are also generally more active and exploratory in the laboratory than females (Young *et al.*, 2010), which could lead to greater encounter rates with passive sampling gear. In its native range, however, operational sex ratio favours females (1.6–1.9 females per male from 1961 to 1975) (Kovtun, 1980). Kovtun (1980) further reports a linear relationship between operational sex ratio and the percentage of eggs surviving to the young-of-the-year stage, with greater survival at lower female:male ratios. Given the vast differences in sex ratio, it would be inappropriate to extrapolate Kovtun's (1980) relationship to the Great Lakes; nevertheless, this relationship suggests that lower female:male ratios may be beneficial in introduced populations.

AGE AND GROWTH

Neogobius melanostomus growth rates are highly variable and site specific. Sources agree that males are larger than females at all ages except age 0 years. They exhibit

greater size at age in its native range (Azov, Black and Caspian Seas) than in the Laurentian Great Lakes, potentially due to saline *v.* fresh water (Corkum *et al.*, 2004; Stepien & Tumeo, 2006). Invasive *N. melanostomus* in the southern Baltic Sea are reported to have a longer life span (up to age 6 years) and larger size at age than most *N. melanostomus* populations (Sokołowska & Fey, 2011), further suggesting larger sizes in saline water. Nevertheless, substantial variation in size at age occurs in both regions (Table I). Reduced size at age in the Laurentian Great Lakes is probably because both males and females reach sexual maturity 1 year earlier than in its native range, potentially contributing to rapid population growth (MacInnis & Corkum, 2000b). Publications reporting *N. melanostomus* lengths use L_T (nose tip to end of caudal fin) or L_S (nose tip to end of caudal peduncle), making comparisons between such datasets difficult. To enable cross-study comparisons, a linear relationship was calculated between L_T and L_S (Table I).

PARASITES AND DISEASE

The parasite fauna of *N. melanostomus* has received close attention in both its native and invaded range. At least 94 species of parasites are known for *N. melanostomus* (Kvach & Stepien, 2008), but new parasite records emerge as the species increases its range (Kosuthova *et al.*, 2009; Francová *et al.*, 2011; Pazooki *et al.*, 2011). In the introduced Eurasian and North American populations, *N. melanostomus* has often acquired local parasites; thus far it has not been reported to harbour invasive parasites into invaded areas (Muzzal *et al.*, 1995; Camp *et al.*, 1999; Rolbiecki, 2006; Kvach & Stepien, 2008; Francová *et al.*, 2011). Other neogobiid species (*B. gymnotrachelus* and *N. fluviatilis*), however, have recently introduced one parasite taxon, *Gyrodactylus proterorhini*, to an invaded river in Poland (Mierzejewska *et al.*, 2011) but in North America adult parasites appear to be poorly adapted to use gobiids as hosts (Kvach & Stepien, 2008). Trematodes are the most common parasitic group of *N. melanostomus* (Kvach & Stepien, 2008), but cestodes (French *et al.*, 2005) and acanthocephalans (Kvach & Stepien, 2008), among other groups, are also commonly found. Larger and older *N. melanostomus* usually have more parasites than younger fish (Ozer, 2007), but parasite prevalence and abundance is generally low (Camp *et al.*, 1999). The consequences of parasitism on *N. melanostomus* are yet to be studied, but infection by the nematode parasite *Eustrongylides excisus* may have made them more susceptible to predation by dice snakes *Natrix tessellate* in Lake Sinoe, Romania (Sloboda *et al.*, 2010). It is yet unknown how *N. melanostomus* parasite loads may affect species predating on *N. melanostomus*, although (Robinson *et al.* 2009) it makes a loose association between *N. melanostomus* diet and *Contracaecum* sp. parasitism in double-crested cormorants *Phalacrocorax auritus*.

Neogobius melanostomus is also a known host of viral haemorrhagic septicaemia virus (VHSV) in the Great Lakes (Al-Hussiney *et al.*, 2011). While there is no evidence linking consumption of *N. melanostomus* to VHSV occurrence in predatory fishes, VHSV can be transmitted to predators through the gut following ingestion of an infected prey item (Meyers & Winton, 1995). Given the growing importance of *N. melanostomus* as prey for piscivorous fishes, further research into the incidence of VHSV in *N. melanostomus* is warranted.

TABLE I. Size at age of *Neogobius melanostomus* reported from selected sites. All values represent mean total length (L_T) at age as assessed from captured individuals unless otherwise indicated (§, backcalculated L_T). Lengths reported in the literature as standard length (L_S) were converted to L_T using the following equation: $L_T = 1.1977 L_S + 0.4586$ ($r^2 = 0.9932$, $n = 193$ individuals from Bailey's Harbor, Lake Michigan and Keweenaw River, Wisconsin, summer 2010). See Sokolowska & Fey (2011) for additional information on age and growth from invasive populations

Region	Age (years)						Source
	0	1	2	3	4	5	
	L_T (mm)						
Males							
Central Basin Lake Erie*	54.5	74.6	104.0	148.0	176.6	n/a	Johnson <i>et al.</i> (2005a)
Upper Detroit River†‡	n/a	75.7	91.4	n/a	n/a	n/a	MacInnis & Corkum (2000b)
Hammond Bay, Lake Huron*§‡	n/a	45.0	72.1	86.9	97.5	105.4	French & Black (2009)
Harbor Beach, Lake Huron*§‡	n/a	40.0	61.4	77.0	88.7	97.4	French & Black (2009)
Southern Black Sea	n/a	106.8	140.0	161.9	182.7	190.0	Gümiş & Kurt (2009)
Gulf of Gdansk§	n/a	n/a	119	136	146	155	Sokolowska & Fey (2011)
Vistula Lagoon§	n/a	87	135	169	n/a	n/a	Pliszka (2002)
Kuibyshev Reservoir§	78	120	133	157	n/a	n/a	Shemonaev & Kirilenko (2009)
Females							
Central Basin Lake Erie*	49.0	70.2	90.3	129.8	n/a	n/a	Johnson <i>et al.</i> (2005a)
Upper Detroit River†‡	n/a	70.4	77.8	99.5	n/a	n/a	MacInnis & Corkum (2000b)
Southern Black Sea	n/a	102.7	129.2	147.1	167.8	182.0	Gümiş & Kurt (2009)
Gulf of Gdansk§	n/a	n/a	94	125	133	144	Sokolowska & Fey (2011)
Vistula Lagoon§	n/a	81	126	157	n/a	n/a	Pliszka (2002)
Kuibyshev Reservoir§	77	105	119	146	n/a	n/a	Shemonaev & Kirilenko (2009)
Unisexed							
Danube River¶‡	50.8	9.7	111.8	n/a	n/a	n/a	Simonović <i>et al.</i> (2001)
Caspian Sea¶‡	54.4	114.2	n/a	n/a	n/a	n/a	Berg (1965)
Azov Sea¶‡	60.3	119.0	139.4	147.8	n/a	n/a	Smirnov (1986)

n/a, not applicable.

*, From *N. melanostomus* captured in late season (September or October); †, mean of *N. melanostomus* captured throughout summer; ‡, L_S reported from source and converted to total length using equation in table legend; §, mean L_T at age from backcalculation from otoliths (not mean from captured individuals); ||, mean of *N. melanostomus* captured from October through to March (no summer); ¶, time of year unknown.

THERMAL, OXYGEN AND SALINITY TOLERANCES

Neogobius melanostomus tolerate a wide range of habitat conditions, potentially contributing to its widespread success. They exhibit a wide salinity tolerance, inhabiting fresh, brackish and marine waters (Skóra *et al.*, 1999; Cross & Rawding, 2009) with a reported salinity tolerance of 40.5 (Moskal'kova, 1996). Nonetheless, there are no known populations in a full ocean habitat (Charlebois *et al.*, 1997) and a recent laboratory experiment found that all *N. melanostomus* died within 48 h under 30 salinity (Ellis & MacIsaac, 2009). This experiment suggests current ballast water exchange regulations, during which ballast tanks are filled with ocean water for *c.* 5 days, may prevent future *N. melanostomus* introduction events (Ellis & MacIsaac, 2009). Oceanic salinities (*c.* 35) appear suitable since *N. melanostomus* are present in high saline (40.6) areas of the Caspian Sea (Kazanchev, 1981), but salts in these habitats are from two distinct molecules (CaSO₄ in the Caspian and Aral Seas and NaCl in the ocean) (Strayer & Smith, 1993). Given the results of Ellis & MacIsaac (2009) and the fact that no ocean populations are known, *N. melanostomus* probably has a salinity tolerance <30 in oceanic (NaCl) waters. A natural test of this hypothesis will unfold in northern Europe, as *N. melanostomus* has a substantial and growing population in the Baltic Sea (brackish water, average salinity of 8), but has not yet colonized the neighbouring North Sea (average salinity 35) [average salinity values after Højerslev *et al.* (1996)].

Neogobius melanostomus also has a wide thermal tolerance, ranging from -1 to 30° C (Moskal'kova, 1996), but prefer warmer water; energetic optimum temperature is estimated to be 26° C (Lee & Johnson, 2005). This may partially explain the disparity in *N. melanostomus* success across the Great Lakes, as the species is most widespread and at its greatest densities in the warmest lake (Erie) and has the smallest range and lowest densities in the coldest (Superior). Water temperature was also significantly higher at stream sites invaded by *N. melanostomus* (mean 23.9° C, *n* = 53) *v.* sites where the species was absent (mean 21.7° C, *n* = 66) (Kornis & Vander Zanden, 2010). Upper thermal limits for the species have been established: the upper limit of positive growth was estimated to be 28.9° C (Lee & Johnson, 2005), loss of righting response occurred at a mean \pm S.E. of 31.5 \pm 0.46° C and mean \pm S.E. critical thermal maximum temperature (T_{cmax}) was 33.4 \pm 0.30° C (Cross & Rawding, 2009).

Neogobius melanostomus are tolerant of very low dissolved oxygen levels, but may attempt to escape hypoxic conditions. Critical lethal threshold values range from 0.4 to 1.3 mg l⁻¹ (Charlebois *et al.*, 1997). They are known to vacate areas *c.* 4 mg l⁻¹, suggesting hypoxia could limit growth rate by increasing activity costs (Arend *et al.*, 2011). Seasonal hypoxia in Lake Erie overlaps with the mid to late-summer growth period, and bioenergetics models suggest this can have a dramatic effect on habitat quality by lowering growth rate potential (Arend *et al.*, 2011).

HABITAT PREFERENCES

Neogobius melanostomus spawn, feed and hide in hard substrata and are typically most abundant in rocky habitats. Tethering experiments in sandy habitat with and without shelters indicated that open habitats (sand and mud) posed a higher risk of predation than sheltered habitat (cobble and boulder) (Belanger & Corkum, 2003) and several field surveys found *N. melanostomus* prefers rocky substrata (Ray

& Corkum, 2001; Young *et al.*, 2010). Nonetheless, soft substrata are utilized by *N. melanostomus* and abundance may be similar on soft and hard substrata in some areas (Johnson *et al.*, 2005b; Taraborelli *et al.*, 2009). Thus, mud and sand habitat are not resistant to invasion and the lack of a hard substratum will not prevent colonization, although *N. melanostomus* will probably colonize hard before soft substrata. In Lakes Michigan and Erie, adults were more abundant on rock while juveniles were more abundant on sand, leading to the hypothesis that adults displace juveniles to sub-optimal habitats (Charlebois *et al.*, 1997; Ray & Corkum, 2001). This hypothesis is logical, albeit not uniformly supported (Taraborelli *et al.*, 2009).

Neogobius melanostomus abundance may correlate with depth and density of aquatic vegetation. Along the shorelines of Lakes Michigan and Huron, it was more abundant in deeper habitat (0.65 m) than shallow (0.38 m) (Cooper & Ruetz, 2009), while in the Bay of Quinte (Lake Ontario) *N. melanostomus* was more abundant at depths of 1.5–3 m relative to 3–5 and 5–7 m (Taraborelli *et al.*, 2009). Thus, *N. melanostomus* appears to avoid the shallow surf zone, but ultimately prefers shallower water (0.7–3 m) over deeper depths during the summer spawning season. This is supported by data from Lake Erie, where mean *N. melanostomus* density was 3.8 times greater in nearshore *v.* offshore habitat from 1995 to 2002, although 55.6% of the overall population occurred offshore due to greater area (Johnson *et al.*, 2005a). *Neogobius melanostomus* migrates offshore during winter and has been recorded as deep as 130 m during April sampling in Lake Ontario (Walsh *et al.*, 2007). Abundance was positively correlated with submerged aquatic vegetation in coastal lakes and drowned river mouths (Cooper & Ruetz, 2009), but no correlation was found between sparse and moderately vegetated habitats in the Bay of Quinte (Taraborelli *et al.*, 2009).

SAMPLING METHODS

Several methods exist for sampling *N. melanostomus*; the most appropriate method will depend on the specific goals of the research project, as each gear type has its own advantages and disadvantages. Active methods include electrofishing, kick seining, trawling, angling and visual assays (scuba or remotely operated video). Backpack and towboat electrofishing can be used to consistently capture *N. melanostomus* in clear, wadeable water, although this method requires the operator to focus on searching for fish on the bottom and may be aided by overturning rocks, as *N. melanostomus* lacks a swimbladder and does not float when electrofished (Phillips *et al.*, 2003; Kornis & Vander Zanden, 2010). Beach seining is inefficient at sampling the preferred rocky habitat, but kick seining, whereby a short (*c.* 2 m) seine is placed downstream of rocky habitat to collect fish as the rocky habitat is disturbed by kicking, has proven effective (Jude *et al.*, 1995). Bottom trawling effectively captures *N. melanostomus* from non-wadeable habitats (Clapp *et al.*, 2001) and is often useful because annual trawling efforts at various sites provide long-term baseline data. Visual methods such as scuba video transects were identified by a method comparison study as optimal for assessing *N. melanostomus* size and density across a wide range of substratum types (Johnson *et al.*, 2005b). Johnson *et al.* (2005b) also identifies angling and bottom trawling as the most effective methods for obtaining specimens from non-wadeable habitat. Methods have also been established to estimate the density of large (>50 mm L_T) *N. melanostomus* via depletion angling surveys (Gutowsky *et al.*, 2011).

Passive methods include minnow traps, fyke nets, gillnets and trotlines, and their efficacy has been the subject of debate. Minnow traps and other similar methods (tyre sampler, torpedo sampler, tube sample and Windermere trap) were classified as extremely inefficient when compared to active methods (Johnson *et al.*, 2005b). In contrast, Kornis & Vander Zanden (2010) found baited (liver) minnow traps to be effective at capturing *N. melanostomus* throughout the summer. Similarly, Diana *et al.* (2006) identified minnow traps as the most cost-effective strategy for capturing *N. melanostomus* in littoral rocky habitat, although gear vulnerability appeared to be heavily influenced by season (868 fish in autumn, zero fish in spring, consistent effort at same sites). Gillnets have been used with moderate success, but Diana *et al.* (2006) also reported seasonal vulnerability to gillnets (11 fish in autumn and 216 fish in spring). Multi-mesh survey gillnets have been employed to capture *N. melanostomus* while also providing an overall picture of the total fish community (Karlson *et al.*, 2007; Almqvist, 2008). Minnow traps are biased towards small *N. melanostomus* while trotlines and gillnets favour larger *N. melanostomus*; by-catch was lower in minnow traps and trotlines than gillnets (Diana *et al.* 2006). Diana *et al.* (2006) also suggest that passive gears are more cost effective than active gears, although active gears were not explicitly tested for capture efficacy by the authors. Passive gears may be inappropriate for certain research goals, such as diet analysis or density estimates.

Several tagging methods have proved effective for marking *N. melanostomus*. Subcutaneously injected latex paint (or visible implant elastomer) was superior to other methods because of ease of use, high visibility, high tag retention (nearly 100% in a recent experiment; M. S. Kornis, unpubl. data) and low mortality (Wolfe & Marsden, 1998). Multiple colours and tagging locations could produce a substantial number of unique combinations to individually identify fish. When it is necessary to individually mark large quantities of fish, floy anchor tags were the most effective technique (0% tag loss), although high mortality rates (50%) are a drawback (Wolfe & Marsden, 1998). Passive integrated transponder (PIT) tags do not cause mortality in *N. melanostomus* and tag retention was reported to be 100%, although growth was reduced in *N. melanostomus* >105 mm (Cookingham & Ruetz, 2008). *Neogobius melanostomus* penned by block nets were difficult to detect with a portable underwater antenna, however, limiting the use of PIT tags in *N. melanostomus* with current technology (Cookingham & Ruetz, 2008).

ECOLOGICAL EFFECTS

Neogobius melanostomus has become an important component of the Laurentian Great Lakes and Baltic Sea food webs by virtue of its high abundance and widespread distribution. The species has had both positive and negative effects on various species through competition, predation and providing forage. Such trophic linkages, particularly with invasive dreissenids (zebra mussel *Dreissena polymorpha* and quagga mussel *Dreissena rostriformis bugensis*), have resulted in several indirect effects, potentially altering nutrient and contaminant pathways (Hogan *et al.*, 2007; Ng *et al.*, 2008) and leading to increased outbreaks of avian botulism (Yule *et al.*, 2006a). Species directly affected from competition with or predation on and by *N. melanostomus* are listed in Tables II, III and IV, while the most important and complex interactions are addressed in more detail below.

TABLE II. Species affected by competition from *Neogobius melanostomus*. Competition may affect species not included in this table, as any species that relies on benthic invertebrates would have diet overlap with *N. melanostomus*. Several species in this table, particularly North American species, were also included in Poos *et al.* (2010)

Region	Species	Evidence	Sources
Laurentian Great Lakes	Mottled sculpin <i>Cottus bairdii</i>	Diet overlap, decreased abundance, laboratory studies (territoriality)	Dubs & Corkum (1996), Janssen & Jude (2001), Lauer <i>et al.</i> (2004), Bergstrom & Mensinger (2009)
	Slimy sculpin <i>Cottus cognatus</i>	Suspected from habitat and diet overlap, laboratory studies (diet)	Chotkowski & Marsden (1999), MacInnis & Corkum (2000b), Bergstrom & Mensinger (2009)
	Spoonhead sculpin <i>Cottus ricei</i>	Suspected from habitat and diet overlap, laboratory studies (diet)	Bergstrom & Mensinger (2009)
	Deepwater sculpin <i>Myoxocephalus thompsonii</i>	Suspected from habitat overlap	Bergstrom & Mensinger (2009)
	<i>Etheostoma</i> sp.	Suspected from habitat and diet overlap	Jude <i>et al.</i> (1995), Barton <i>et al.</i> (2005), Carman <i>et al.</i> (2006)
	Johnny darter <i>Etheostoma nigrum</i>	Diet overlap, decreased abundance, habitat overlap	Corkum <i>et al.</i> (1998), Lauer <i>et al.</i> (2004)
	Rainbow darter <i>Etheostoma caeruleum</i>	Direct observation, presence/absence field studies	French & Jude (2001), Diggins <i>et al.</i> (2002), Krakowiak & Pennuto (2008)
	<i>Noturus</i> sp.	Suspected from habitat and diet overlap	MacInnis & Corkum (2000b)
	Brindled madtom <i>Noturus miurus</i>	Suspected from habitat and diet overlap	Corkum <i>et al.</i> (1998), MacInnis & Corkum (2000b)
	Northern madtom <i>Noturus stigmosus</i>	Direct observation	MacInnis & Corkum (2000b), French & Jude (2001)
	Tadpole madtom <i>Noturus gyrinus</i>	Suspected from habitat and diet overlap	Poos <i>et al.</i> (2010)

TABLE II. Continued

Region	Species	Evidence	Sources
Baltic Sea	Stonecat <i>Noturus flavus</i>	Suspected from habitat and diet overlap	Kornis, field observation
	<i>Percina</i> sp.	Suspected from habitat and diet overlap	Jude <i>et al.</i> (1995), Barton <i>et al.</i> (2005), Carman <i>et al.</i> (2006)
	Logperch <i>Percina caprodes</i>	Decreased abundance, habitat and diet overlap, laboratory studies (diet, territoriality)	French & Jude (2001), Balshine <i>et al.</i> (2005), Bergstrom & Mensinger (2009)
	Juvenile yellow perch <i>Perca flavescens</i>	Habitat and diet overlap	Duncan <i>et al.</i> (2011)
	European flounder <i>Platichthys flesus</i>	Diet overlap, decreased abundance	Karlson <i>et al.</i> (2007)
	Eelpout <i>Zoarces viviparus</i>	Suspected from diet overlap	Skóra & Rzeznik (2001)
	European eel <i>Anguilla anguilla</i>	Suspected from diet overlap	Skóra & Rzeznik (2001)
	Perch <i>Perca fluviatilis</i>	Suspected from diet overlap	Skóra & Rzeznik (2001)
	Roach <i>Rutilus rutilus</i>	Suspected from diet overlap	Skóra & Rzeznik (2001)
	Vimba bream <i>Vimba vimba</i>	Suspected from diet overlap	Skóra & Rzeznik (2001)

TABLE III. Prey items of *Neogobius melanostomus*. All diet data are reported as % wet mass, % dry mass or % volume to allow for comparisons across studies. Two references from Eurasia are exceptions (references 15 and 16, % unknown and % index of relative importance, respectively), but were included because papers from this region were less prevalent. Due to ontogenetic diet shifts, diet data have been separated by size class when available and a mean size is provided if data are aggregated to all size classes. Mean \pm s.d. are provided for each of the three regions; an overall mean for all three regions combined is also provided. Some studies distinguished between molluscs (bivalves and gastropods), crustaceans (amphipods, isopods, barnacles and decapods) and other benthos (Diptera, Ephemeroptera, Trichoptera and Polychaeta) while others lumped these taxa. To allow comparison, specific taxa are listed when available, but also provide lumped data (total) categories equal to the sum of the appropriate taxa. Percentages may not sum to 100 due to rounding error

System	Year	Metric	L_T (mm)	n	Molluscs				Crustacea				Prey items				Other benthos		Non-benthos		References						
					Dreis.		Oth.		Amph.		Isop.		Barn.		Oth.		Total		Dipt	Ephem.		Trich.	Poly.	Oth.	Total	Zoop.	Fishes
					Total		Total		Total		Total		Total		Total												
Laurentian Great Lakes																											
Nearshore	1992–2005	% Wet mass	30–70	530	34	4	38	13	0	0	0	0	0	0	0	13	6	0	0	6	0	10	22	27	0	1	
Lake Erie																											
Nearshore	1992–2005	% Wet mass	70–110	488	58	6	64	8	0	0	0	0	0	0	0	8	4	0	0	4	0	6	14	13	1	1	
Lake Erie																											
Nearshore	1992–2005	% Wet mass	>110	236	75	6	81	5	0	0	0	0	0	0	0	5	4	0	0	3	0	4	11	3	0	1	
Lake Erie																											
Offshore Lake Erie	1992–2005	% Wet mass	30–70	238	28	7	35	18	0	0	0	0	0	0	0	18	7	0	0	8	0	13	28	19	0	1	
Offshore Lake Erie																											
Offshore Lake Erie	1992–2005	% Wet mass	70–110	198	39	12	51	12	0	0	0	0	0	0	0	12	16	0	0	6	0	8	30	5	0	1	
Offshore Lake Erie																											
Offshore Lake Erie	1992–2005	% Wet mass	>110	102	37	6	43	13	0	0	0	0	0	0	0	13	24	0	0	6	0	9	39	3	2	1	
Eastern Lake Erie	2001, 2003	% Dry mass	<100	37	52.6	34.2	86.8	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	2	
Eastern Lake Erie																											
Eastern Lake Erie	2001, 2003	% Dry mass	100–150	57	88.1	11.8	99.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Eastern Lake Erie																											
Eastern Lake Erie	2001, 2003	% Dry mass	>150	37	99.2	0.8	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Southern Lake Michigan	1994	% Volume	<60	27	8	0	8	21	18	0	0	40	21	0	0	0	0	0	0	0	0	0	0	24	0	3	
Calumet Harbor																											

TABLE III. Continued

System	Year	Metric	L_T (mm)	Prey items																	
				Molluscs				Crustacea				Other benthos				Non-benthos					
				<i>n</i>	Dreis.	OthM.	Total	Total	Amph.	Isop.	Barn.	OthC.	Total	Dipt	Ephem.	Trich.	Poly.	OthB.	Total	Zoop.	Fishes
Southern Lake Michigan Calumet Harbor	1994	% Volume	>60	25	68	0	68	6	4	0	18	22	0	0	0	0	0	0	0	0	3
Lake Ontario Mexico Bay	2007	% Dry mass	All (average = 58)	100	9.7	0	9.7	6.5	0	0	0	6.5	60.1	0	0	0	2.5	62.6	21.0	0	4
Mean \pm s.d.	n/a	%	All	2076	49.7 \pm 29.1	7.3 \pm 9.5	57.0 \pm 31.7	8.5 \pm 6.9	1.9 \pm 5.4	0.0 \pm 0.0	1.5 \pm 5.1	11.4 \pm 11.3	12.9 \pm 17.0	0.0 \pm 0.0	2.8 \pm 3.2	0.0 \pm 0.0	4.4 \pm 4.7	17.3 \pm 14.3	9.6 \pm 10.5	0.3 \pm 0.6	n/a
Rivers in the Laurentian Great Lakes watershed																					
St Clair River	1993	% Volume	All (mean = 68)	31	11.4	47.7	59.1	0	0	0	0	0	22.7	0	2.3	0	9.1	34.1	6.8	0	5
St Clair River	1994	% Volume	35–74	186	13.1	14.7	27.8	0	0	0	7.6	7.6	25.7	17.5	19.7	0	10	63.9	0	0.9	6
St Clair River	1994	% Volume	≥ 75	118	35.3	13.9	49.2	0	0	0	4.3	4.3	7.9	22.7	14.3	0	0.1	45.0	0	1.5	6
Tributaries (5) of Lake Michigan	2007	% Wet mass	All (average = 61)	30	0	17.1	17.1	4.8	0.2	0	0	5.0	53.5	8.8	10.6	0	5.0	77.9	0	0	7
Tributaries (4) of Lake Erie	2000, 2001	% Volume	30–44	72	0	0	0	0	0	0	0	0	64	21	12	0	3	100	0	0	8
Tributaries (4) of Lake Erie	2000, 2001	% Volume	45–59	123	0	0	0	0	0	0	0	0	56	32	8	0	5	100	0	0	8

TABLE III. Continued

System	Year	Metric	L _T (mm)	n	Prey items																	
					Molluscs			Crustacea				Other benthos				Non-benthos						
					Dreis.	OthM.	Total	Amph.	Isop.	Bam.	OthC.	Total	Dipt	Ephem.	Trich.	Poly.	OthB.	Total	Zoop.	Fishes	References	
Tributaries (4) of Lake Erie	2000, 2001	% Volume	60–74	76	0	0	0	0	0	0	0	0	0	53	32	10	0	6	100	0	0	8
Tributaries (4) of Lake Erie	2000, 2001	% Volume	≥ 75	49	0	0	0	0	0	0	0	0	0	40	50	7	0	3	100	0	0	8
Ellicott Creek Tributaries of Lake Erie	2007	% Wet mass	All	25	0	13.1	13.1	66.0	0	0	0	66.0	2.0	0.2	3.4	0	15.4	21.0	0	0	0	9
Mean ± s.d.	n/a	%	All	710	6.6 ± 12.0	11.8 ± 15.4	18.5 ± 22.6	7.9 ± 21.9	0.0 ± 0.1	0.0 ± 0.0	1.3 ± 2.8	9.2 ± 21.5	36.1 ± 22.4	20.5 ± 16.3	9.7 ± 5.4	0.0 ± 0.0	5.3 ± 4.7	71.3 ± 31.6	0.8 ± 2.3	0.3 ± 0.6	n/a	
Eurasian waters including native range, Baltic Sea and invaded rivers																						
Baltic Sea (Gdansk)	2004	% Dry mass	60–120	147	0	69.6	69.6	0	0	1.6	0	1.6	0	0	0	29.4	0	29.4	0	0	10	
Baltic Sea (Gdansk)	2004	% Dry mass	120–140	98	0	78.5	78.5	0.3	0	4.2	0	4.5	0	0	0	16.9	0	16.9	0	0	10	
Baltic Sea (Gdansk)	2004	% Dry mass	>140	78	0	88.9	88.9	2.1	0	0.4	0	2.5	0	0	0	7.1	0	7.1	0	1.6	10	
Baltic Sea (Gdansk)	1995–1996	% Dry mass	All	152	0	65.3	65.3	3.2	25.4	0	0	28.6	0	0	0	6.1	0	6.1	0	0	11	
Baltic Sea (Denmark)	2010	% Wet mass	75–102	48	0	87.0	87.0	0	4	0	9*	11	0	0	0	0	0	0	0	0	17	
Baltic Sea (Denmark)	2010	% Wet mass	103–132	279	0	356	35.6	0.4	0.4	0	61.4*	62.2	0	0	0	0	0	0	0	2.2	17	
Baltic Sea (Denmark)	2010	% Wet mass	133–170	147	0	22.7	22.7	0	0.2	0	72.4*	72.6	0	0	0	0	0	0	0	4.7	17	

TABLE III. Continued

System	Year	Metric	L_T (mm)	<i>n</i>	Molluscs			Prey items										Non-benthos		
					Dreis.	OthM.	Total	Amph.	Isop.	Barn.	OthC.	Total	Dipt	Ephem.	Trich.	Poly.	OthB.	Total	Zoop.	Fishes
Azov Sea	Pre-1964	% Dry mass	All	n/a	n/a	n/a	51	n/a	n/a	n/a	0	18	0	0	0	30	0	30	0	12
Azov Sea	1968–1972	% Dry mass	All	n/a	n/a	n/a	85.3	n/a	n/a	n/a	0	6.9	n/a	0	0	2.5	0	2.5	0	4.8
Danube River	2007	% Wet mass	All	554	1.4	13.9	15.3	46.5	8.5	0	0	55	25.4	0.1	0.6	0	3.5	29.6	0	14
Hungary Danube River	1998	% Unknown	All	13	Most of tot.	Some of tot.	70.6	n/a	n/a	n/a	n/a	26	n/a	n/a	n/a	n/a	3.4	3.4	0	15
Serbia Black Sea	2004–2006	% IRI	All	211	0	55.7	55.7	05	0	0	0	0.5	0	0	0	19.8	4.9	24.7	0	19
Romania	n/a	%	All	699	0.2 ± 0.6	62.0 ± 26.1	64.5 ± 22.3	9.5 ± 18.2	5.7 ± 10.3	1.0 ± 1.7	0.0 ± 0.0	16.0 ± 18.1	3.6 ± 9.6	0.0 ± 0.0	0.1 ± 0.2	14.0 ± 11.8	1.3 ± 2.0	16.6 ± 12.0	0.0 ± 0.0	2.8 ± 6.3
Overall mean diets across regions				3485	23.9 ± 29.3	21.4 ± 26.4	47.5 ± 31.3	7.7 ± 14.6	1.9 ± 5.8	0.2 ± 0.8	1.3 ± 3.6	11.4 ± 16.0	18.1 ± 20.5	7.0 ± 12.9	4.9 ± 6.0	3.5 ± 8.3	3.7 ± 4.3	32.8 ± 32.3	3.9 ± 7.8	1.0 ± 3.4

L_T , total length; n/a, data were not available; *, other Crustacea identified as shrimp (decapods); Dreis., dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*); OthM., other molluscs, typically native (includes bivalves and gastropods); Amph., Amphipoda (typically gammarids); Isop., Isopoda; Barn., barnacles; OthC., other crustacea (usually unidentified); Dipt., Diptera (predominantly Chironomidae); Ephem., Ephemeroptera; Trich., Trichoptera; Poly., Polychaeta; OthB., other benthos (usually unidentified); Zoop., Zooplankton (usually dominated by cladocerans but includes copepods and bythotrephes); 1, Johnson *et al.* (2005a); 2, Barton *et al.* (2005); 3, Janssen & Jude (2001); 4, Johnson *et al.* (2008); 5, Jude *et al.* (1995); 6, French & Jude (2001); 7, M. S. Kornis, unpubl. data; 8, Phillips *et al.* (2003); 9, Pennuto *et al.* (2010); 10, Karlson *et al.* (2007); 11, Skóra & Rzeznik (2001); 12, Svetovidov (1964); 13, Kovun *et al.* (1974); 14, Borza *et al.* (2009); 15, Simonović *et al.* (1998); 16, Bănuș & Harnelin-Vivien (2009); 17, Azour 2011.

TABLE IV. Predators of *Neogobius melanostomus* identified in the literature but there may be others

Predator	Region	Per cent of diet (if provided)	Source(s)
Baltic Sea Cod <i>Gadus morhua</i>	Baltic Sea (Gulf of Gdansk)	Consumption was highly variable across season, L_T class and <i>N. melanostomus</i> abundance at sampling site; 22.4% by mass overall	Almqvist <i>et al.</i> (2010)
Perch <i>Perca fluviatilis</i>	Baltic Sea (Gulf of Gdansk)	40.7, 77 and 96.3% by mass in 100–150, 150–200 and 200–250 mm L_T classes, respectively; 69.2% by mass overall	Almqvist <i>et al.</i> (2010)
Great cormorants <i>Phalacrocorax carbo</i>	Baltic Sea	60–70% by number before 14 April and 90% by number in late season	Bzoma (1998)
Grey heron <i>Ardea cinerea</i>	Baltic Sea	95% by number	Jakubas (2004)
Turbot <i>Scophthalmus maximus</i>	Baltic Sea	Not provided	Sapota & Skóra (2005)
Laurentian Great Lakes Brown trout <i>Salmo trutta</i> Burbot <i>Lota lota</i>	Lake Erie Lakes Michigan, Huron and Erie	c. 10–15% 75% by mass	Campbell <i>et al.</i> (2009) Johnson <i>et al.</i> (2005a), Hensler <i>et al.</i> (2008) Jacobs <i>et al.</i> (2010)
Burbot <i>L. lota</i>	Northern Lake Michigan	16.1, 33.5 and 15.4% in 200–399, 400–599 and 600–799 mm L_T classes; 24.6% by mass overall)	
Double-crested cormorant <i>Phalacrocorax auritus</i> (chick)	Lake Ontario (Hamilton Harbour)	1.8–21% by number of regurgitated chick diet; 10.5–23.5% of nests had <i>N. melanostomus</i> (10.5% excludes nests with specimens that were probably <i>N. melanostomus</i> but were not positivity identified)	Somers <i>et al.</i> (2003)
Double-crested cormorant <i>P. auritus</i> (adult)	Eastern Lake Ontario	79.4% by number over the course of the season (includes pre-chick, chick and post-chick time frames)	Johnson <i>et al.</i> (2010)

TABLE IV. Continued

Predator	Region	Per cent of diet (if provided)	Source(s)
Freshwater drum <i>Aplodinotus grunniens</i>	Lake Erie	Not provided	Campbell <i>et al.</i> (2009)
Ictaluridae (catfishes and bullheads)	Great Lakes and tributaries	Not provided, suspected as ictalurids are benthic-oriented predators	
Lake Erie watersnake <i>Nerodia sipedon insularum</i>	Lake Erie	>92% by number.	King <i>et al.</i> (2006)
Lake trout <i>Salvelinus namaycush</i>	Lake Ontario (Kingston Basin)	0, 0, 7.9, 56.8, 8.9 and 0% by mass in 250–349, 350–449, 450–549, 550–649, 650–749 and 750–849 mm L_T classes, respectively; 36.2% by mass and 19.9% by number overall	Dietrich <i>et al.</i> (2006)
Lake trout <i>S. namaycush</i>	Northern Lake Michigan	1.7% by mass overall	Jacobs <i>et al.</i> (2010)
Lake whitefish <i>Coregonus clupeaformis</i>	Northern Lake Michigan	Not provided	M. S. Kornis, unpubl. data
Pike <i>Esox lucius</i>	St Lawrence River	25.4% of stomachs contained <i>N. melanostomus</i> , 10.9% contained only <i>N. melanostomus</i>	Reyjol <i>et al.</i> (2010)
Northern watersnake <i>Nerodia sipedon</i>	Lake Erie	Not provided	King <i>et al.</i> (2006)
Rock bass <i>Ambloplites rupestris</i> and <i>Ambloplites constellatus</i>	St Clair River	Not provided	Jude <i>et al.</i> (1995)
Sauger <i>Sander canadensis</i>	St Lawrence River	64.5% of stomachs contained <i>N. melanostomus</i> , 53.2% contained only <i>N. melanostomus</i> .	Reyjol <i>et al.</i> (2010)
Smallmouth bass <i>Micropterus dolomieu</i> (adult)	Lake Erie	75% by dry mass	Johnson <i>et al.</i> (2005b)

TABLE IV. Continued

Predator	Region	Per cent of diet (if provided)	Source(s)
Smallmouth bass <i>M. dolomieu</i> (YOY)	Lake Erie	0, 23, 43, 62 and 79% by mass in 21–40, 41–60, 61–80, 81–100 and 101–155 mm L_T classes, respectively	Steinhart <i>et al.</i> (2004b)
Stonecat <i>Noturus flavus</i>	St Clair River	Not provided	Jude <i>et al.</i> (1995)
Tubenose gobies <i>Proterorhinus marmoratus</i>	St Clair River	Not provided	Jude <i>et al.</i> (1995)
Walleye <i>Sander vitreus</i>	Lake Erie	10% by dry mass	Johnson <i>et al.</i> (2005a)
Walleye <i>S. vitreus</i>	Lake Erie	c. 10–15%	Campbell <i>et al.</i> (2009)
White bass <i>Morone chrysops</i>	Lake Erie	15% by dry mass	Johnson <i>et al.</i> (2005a)
White perch <i>Morone americana</i>	Lake Erie	c. 10–15%	Campbell <i>et al.</i> (2009)
Yellow perch <i>Perca flavescens</i>	Southern Lake Michigan	10.2, 33.3, 68.9 and 38.8% by volume in 100–119, 120–159, 160–189 and > 189 mm L_T classes, respectively	Truemper <i>et al.</i> (2006)
Yellow perch <i>P. flavescens</i>	Lake Erie	25–30% by dry mass (c. value for every year since 1998)	Johnson <i>et al.</i> (2005a), Campbell <i>et al.</i> (2009)

YOY, young-of-the-year; L_T , total length; not provided, no quantitative data were presented by the study. Such studies either anecdotally mentioned a certain species preyed on *N. melanostomus* or provided stable-isotope data linking the predator to *N. melanostomus*.

COMPETITION

Neogobius melanostomus competes with many species (Table II) through resource competition, spawning interference and displacement of native species to sub-optimal habitat. Laboratory evidence suggests that sensory abilities are comparable with native species despite the *N. melanostomus* superficial neuromasts (Bergstrom & Mensinger, 2009). Nonetheless, *N. melanostomus* dominated food resources in laboratory experiments with three native species of fishes, suggesting native species suffer from resource competition (Bergstrom & Mensinger, 2009). Spawning interference is illustrated by laboratory experiments in which *N. melanostomus* attacked nest-guarding mottled sculpins *Cottus bairdii* Girard 1850, occupied their nest, changed to black spawning colouration and caused loss of nearly all *C. bairdii* eggs (Janssen & Jude, 2001). Displacement of native species is also supported by laboratory experiments in which aggressive *N. melanostomus* oust resident *C. bairdii* (Dubs & Corkum, 1996) and logperch *Percina caprodes* (Rafinesque 1818) (Balshine *et al.*, 2005) from shelters, running counter to the common behavioural finding that residents typically defeat challengers in territory disputes (Balshine *et al.*, 2005).

These mechanisms, elucidated in the laboratory, probably explain observed changes in native fish abundance and diversity at some sites. In the Laurentian Great Lakes, both *C. bairdii* and Johnny darter *Etheostoma nigrum* Rafinesque 1820 rapidly declined in trawl catches following the invasion of *N. melanostomus* at three nearshore sampling stations in southern Lake Michigan (Lauer *et al.*, 2004) and *C. bairdii* was almost completely extirpated from Calumet Harbor 4 years after the discovery of *N. melanostomus* (Janssen & Jude, 2001). *Neogobius melanostomus* are starting to colonize deeper waters and may soon threaten deepwater sculpin *Myoxocephalus thompsonii* (Girard 1851) and spoonhead sculpin *Cottus ricei* (Nelson 1876) as well (Bergstrom & Mensinger, 2009). In Lake Erie tributaries, taxa richness, Shannon diversity, CPUE (catch per unit effort) and BPUE (biomass per unit effort) of native fishes did not differ between *N. melanostomus*-absent and *N. melanostomus*-present streams ($P > 0.05$, d.f. = 5), although each metric was lower in *N. melanostomus*-present streams (Krakowiak & Pennuto, 2008).

Nevertheless, competitive interactions probably vary across space, as supported by studies showing that *C. bairdii* and *E. nigrum* are not always extirpated after *N. melanostomus* invasion. In Lake Huron's deepwater demersal community, all common species decreased in abundance from early (1976–1991) to late (1994–2006) periods except for spottail shiner *Notropis hudsonius* (Clinton 1824) and *E. nigrum* (which had no change) and *N. melanostomus* (which increased) (Riley *et al.*, 2008). Additionally, increased *N. melanostomus* CPUE in 20 Wisconsin streams correlated with decreased *E. nigrum* CPUE from 2007 to 2010, but CPUE of four other benthic fishes [*C. bairdii*, blackside darter *Percina maculata* (Girard 1859), fantail darter *Etheostoma flabellare* Rafinesque 1819 and *P. caprodes*] did not differ over the same time span (M. S. Kornis, unpubl. data). Factors such as population density, water temperature, forage availability and habitat availability probably contribute to variability in the degree of effect on native fishes.

Neogobius melanostomus threatens several species with conservation concerns. In several species-at-risk hotspots in Ontario tributaries, recently established *N. melanostomus* populations threaten seven endangered species (one fish and six mussels) in addition to 16 non-endangered benthic fish species (Poos *et al.*, 2010).

Neogobius melanostomus is also abundant in several tributaries occupied by species listed as critically imperilled or imperilled in Wisconsin, including three species of mussel and three species of aquatic insect (M. S. Kornis, pers. obs.). Mussel species are affected both through direct predation and indirectly through reduced availability of native fish hosts required by some mussel species for their glochidia larvae (Poos *et al.* 2010). Poos *et al.* (2010) provide an excellent summary of native fishes affected by *N. melanostomus* (incorporated into Table II).

In the Baltic Sea, *N. melanostomus* primarily competes with the commercially important flounder *Platichthys flesus* L. 1758, evidenced by strong similarities in diet and a negative correlation between *P. flesus* and *N. melanostomus* abundance (Karlson *et al.*, 2007). *Neogobius melanostomus* also restricts habitat utilization and therefore food availability to *P. flesus* (Karlson *et al.*, 2007). Three-spined stickleback *Gasterosteus aculeatus* L. 1758 abundance in the Gulf of Gdansk was also negatively correlated with *N. melanostomus* abundance, indicating a shift from pelagic to benthic forage fishes as *N. melanostomus* populations increase in size (Corkum *et al.*, 2004).

PREY

Neogobius melanostomus feeds on many taxa including zooplankton (as juveniles), benthic invertebrates, small fishes and the eggs and larvae of large fishes (Table III). Diets are influenced by habitat, time of day and year and body size. In lakes and seas (lentic habitats), molluscs are usually the primary diet component (mean of 57.0 and 64.5% by mass in the Laurentian Great Lakes and Eurasia, respectively). In a laboratory study, however, *N. melanostomus* that were fed only dreissenids had lower growth rates (-0.04 g day^{-1}) than those fed only chironomids (0.13 g day^{-1}), suggesting dreissenids may be primarily consumed when more profitable prey are rare or difficult to capture (Coulter *et al.*, 2011). *Neogobius melanostomus* can crush mollusc prey with the pharyngeal teeth (Ghedotti *et al.*, 1995) with field studies indicating c. 50% of mussels consumed by *N. melanostomus* are crushed v. 50% swallowed whole (Andraso *et al.*, 2011). Crushed dreissenids were larger than those swallowed whole and consumed mussel length was positively correlated with *N. melanostomus* length, although diet selectivity indices suggest that the greatest preference is for mussels 8–11 mm (Andraso *et al.*, 2011). In at least one lentic habitat, however, decapods (shrimp, *Palaemon* spp.) comprised the greatest percentage by mass of the diets of *N. melanostomus* $>10.3 \text{ cm } L_T$ [61–72%, Danish waters of the Baltic Sea (Azour, 2011)]. In streams (lotic habitats), diets are typically dominated by non-mollusc benthic invertebrates (mean of 71.3% by mass in Laurentian Great Lakes tributaries). Such diet diversity among populations demonstrates *N. melanostomus* is capable of adapting to locally abundant food sources, facilitating the species' invasion potential.

Neogobius melanostomus feeds at all times of day with diet changing on a diel basis. In the Flint River, Michigan, hydropsychid caddisfly and chironomid larvae dominated diets during the day, chironomid pupae during the evening and heptageniid mayflies at night (Carman *et al.*, 2006). Similarly, nocturnal diets shifted away from dreissenids (decreased from 26 to 0% by dry mass) and towards chironomids (increased from 46 to 71%) in Mexico Bay, Lake Ontario (Johnson *et al.*, 2008). The importance of various diet components depends on body size: a mass-balance

dietary simulation (confirmed by gut content data) indicated that chironomids and amphipods were the most energetically important prey to small *N. melanostomus* (<11.2 cm L_T) while dreissenids (specifically *D. rostriformis*) were most important to large *N. melanostomus* (>11.2 cm L_T) in eastern Lake Erie's littoral food web (Campbell *et al.*, 2009). While adult *N. melanostomus* feed heavily on dreissenids in the Great Lakes, dreissenids are not required for *N. melanostomus* populations to thrive. Carman *et al.* (2006) documented abundant *N. melanostomus* populations at river sites lacking dreissenids. These results were substantiated by documentation of extensive invasion of Lake Michigan tributaries (26 of 75 catchments were invaded) by *N. melanostomus* despite the fact that only 13% of invaded streams had dreissenids (Kornis & Vander Zanden, 2010). In aggregate, *N. melanostomus* consume large quantities of food: mean annual prey consumption peaked in Lake Erie at $5.98 \pm 2.17 \times 10^4$ t ($\pm 95\%$ C.I.) wet mass in 1999 (Johnson *et al.*, 2005a).

Several species targeted by conservation efforts may suffer reduced recruitment as a result of egg depredation by *N. melanostomus*. They significantly reduced lake trout *Salvelinus namaycush* (Walbaum 1792) fry emergence success in aquaria experiments by consuming both eggs and fry (Chotkowski & Marsden, 1999; Fitzsimons *et al.*, 2009a), suggesting the potential for depredation in the natural setting, particularly as *N. melanostomus* colonize deeper depths (Schaeffer *et al.*, 2005; Walsh *et al.*, 2007). The combination of *N. melanostomus* predation and colonization of interstitial spaces by dreissenids will render nearshore reefs less optimal habitat for spawning *S. namaycush* (Vanderploeg *et al.*, 2002). Empirical data confirm concerns raised by these studies: *S. namaycush* fry emergence dropped to near zero levels after *N. melanostomus* invaded a *S. namaycush* spawning reef at Port Weller, Lake Ontario (Fitzsimons *et al.*, 2009b). *Neogobius melanostomus* also prey on the eggs of lake sturgeon *Acipenser fulvescens* Rafinesque 1817, a species listed as threatened in North America, with hatch rate increasing from <1 to 16% in predator exclusion chambers (Nichols *et al.*, 2003). In addition to *A. fulvescens* and *S. namaycush*, other desirable fish species vulnerable to egg depredation from *N. melanostomus* include *M. dolomieu* (Steinhart *et al.*, 2004a), walleye *Sander vitreus* (Mitchill 1818) (Roseman *et al.*, 2006) and probably any species with benthic eggs.

PREDATORS

Due to its widespread success and abundance, *N. melanostomus* has become an important forage item for many species in both the Great Lakes and the Baltic Sea (Table IV). Predators with heavy reliance on *N. melanostomus* in the Great Lakes include burbot *Lota lota* (L. 1758), double-crested cormorants *Nerodia sipedon*, watersnakes, yellow perch *Perca flavescens* (Mitchill 1814) and *M. dolomieu*. In the Baltic Sea, main predators include perch *Perca fluviatilis* L. 1758, cod *Gadus morhua* L. 1758, great cormorants *Phalacrocorax carbo* and grey herons *Ardea cinerea*. There is some evidence that high predation levels contribute to control of *N. melanostomus* abundance. Abundance declined from 2004 to 2008 in Lake Erie, coinciding with increased importance of *N. melanostomus* in *L. lota* diets (Madenjian *et al.*, 2011). Bioenergetic models based on *L. lota* diet data, combined with estimates of *L. lota* and *N. melanostomus* abundance, suggest that adult *L. lota* consume 61% (1361 of 2232 t) of the estimated standing stock of *N. melanostomus* in

eastern Lake Erie on an annual basis (Madenjian *et al.*, 2011). Increased predation may therefore contribute to recent stabilizing trends in *N. melanostomus* populations.

Neogobius melanostomus can reach higher numerical densities than native benthic fishes (Lauer *et al.*, 2004; Steinhart *et al.*, 2004a; Johnson *et al.*, 2005a) which often makes it more available to predators. Predators with high reliance on *N. melanostomus* (*L. lota* and *M. dolomieu*) have shown an increase in mean L_T at age while predators with low reliance on *N. melanostomus* [*S. vitreus* and white bass *Morone chrysops* (Rafinesque 1820)] have shown no trend (Johnson *et al.*, 2005a). This suggests an advantage to feeding on *N. melanostomus*, possibly due to high abundance and reduced energetic costs of pursuing and capturing *N. melanostomus* relative to alternative pelagic prey (Johnson *et al.*, 2005a). *Neogobius melanostomus* energy density is comparable with native benthic fishes, although energy density varies in time and space, probably due to a variety of prey types including energy-poor dreissenids (Ruetz *et al.*, 2009). *Neogobius melanostomus* energy density was significantly higher in a Lake Michigan tributary than in central Lake Erie, potentially due to higher consumption of dreissenids in Lake Erie (Ruetz *et al.*, 2009). For the same reason, larger *N. melanostomus* typically have a lower energy density than smaller ones.

Salvelinus namaycush, a species of ecological concern in the Great Lakes, may receive limited benefit from increased reliance on *N. melanostomus* as forage, although the deleterious effects of *N. melanostomus* predation on *S. namaycush* eggs far exceeds any potential dietary benefit. Early mortality syndrome (EMS) in *S. namaycush* is probably due to low thiamine levels caused by forage species [alewife *Alosa pseudoharengus* (Wilson 1811) and rainbow smelt *Osmerus mordax* (Mithcill 1814)] rich in thiaminase, an enzyme that breaks down thiamine (Fisher *et al.*, 1996; Honeyfield *et al.*, 2005). *Neogobius melanostomus* represents a low-thiaminase forage compared to *A. pseudoharengus* in the Great Lakes, and significantly greater survival of *S. namaycush* eggs to hatching stage was observed for eggs taken from *S. namaycush* foraging primarily on *N. melanostomus* (south Lake Michigan) *v.* eggs from *S. namaycush* foraging primarily on *A. pseudoharengus* (north Lake Michigan) (Jaroszewska *et al.*, 2009). North-site adult females also had thiamine concentrations nearly half that of females from the south site (Jaroszewska *et al.*, 2009). Thus, the inclusion of *N. melanostomus* in the diets of *S. namaycush* can potentially ameliorate thiamine deficiency and EMS. Unfortunately, *S. namaycush* consumption of *N. melanostomus* is highly variable by site and in northern Lake Michigan *N. melanostomus* comprise a small portion (1.7% by mass) of *S. namaycush* diets (Jacobs *et al.*, 2010). Models indicate that *N. melanostomus* must comprise at least 25% of *S. namaycush* diet before thiamine deficiency is reduced (Fitzsimons *et al.*, 2009b).

Two species of watersnakes have benefited from a diet shift towards *N. melanostomus*. *Neogobius melanostomus* now comprises the primary prey of both northern watersnakes *Nerodia sipedon* and the federally endangered Lake Erie watersnake *Nerodia sipedon insularum*, with *N. melanostomus* representing >90% of the diet of the latter (King *et al.*, 2006; Jones *et al.*, 2009). Faster growth rates and larger body sizes were observed in Lake Erie watersnakes after the establishment of *N. melanostomus*; the feeding habits of these snakes (rooting around underneath rocky substrata) make *N. melanostomus* a frequently encountered item (King *et al.*, 2006). It is estimated that Lake Erie watersnakes consume 200 000–3 300 000

N. melanostomus (4455–56 178 kg year⁻¹), although this is unlikely to have more than local effects on *N. melanostomus* populations (Jones *et al.*, 2009).

Micropterus dolomieu consume *N. melanostomus* and may select for them under certain conditions. *Micropterus dolomieu* select for *N. melanostomus* [compared with golden shiners *Notemigonus crysoleucas* (Mitchill 1814) and northern crayfish *Orconectes virilise*] at low turbidities (0 and 5 NTU) in a laboratory setting (Carter *et al.*, 2010). Benthic cover (PVC half-pipes placed on bottom of tank) and higher turbidity reduced consumption of *N. melanostomus* to neutral selection (consumed in similar proportion to availability) in favour of *N. crysoleucas* (Carter *et al.*, 2010). Thus, while *N. melanostomus* negatively affect *M. dolomieu* recruitment through egg predation (Steinhart *et al.*, 2004a), they also provide *M. dolomieu* with an abundant forage resource, leading to increased *M. dolomieu* growth rates following *N. melanostomus* establishment (Steinhart *et al.*, 2004b). Stable-isotope data confirmed that *N. melanostomus* was important to the somatic growth of *M. dolomieu* as well as *A. rupestris* and freshwater drum *Aplodinotus grunniens* Rafinesque 1819 (Campbell *et al.*, 2009). Consequently, anglers use *N. melanostomus* as *M. dolomieu* bait, with artificial goby baits offered at tackle shops throughout the Great Lakes (Wickett & Corkum, 1998; M. S. Kornis, pers. obs.). The use of *N. melanostomus* as bait is a potential risk for spreading them, especially to systems outside the Great Lakes basin. Targeted campaigns to prevent spread and regulation limiting the use of angler-captured bait to the water body of capture help mitigate this risk.

FOOD WEB EFFECTS

Neogobius melanostomus has reached large population sizes in many invaded systems, often leading to changes in entire food webs. In both the Great Lakes and the Baltic Sea, high abundance of *N. melanostomus* contributed to the increased success of some fish-eating birds. In the Baltic Sea, high abundance of *N. melanostomus* near one breeding site for *A. cinerea* correlated with a greater than two-fold increase in number of nests from 1999 to 2003 (Jakubas, 2004). At this site, *N. melanostomus* comprised 95% of *A. cinerea* diets by number. Over the same time period, two other *A. cinerea* rookeries (located in areas without *N. melanostomus*) decreased in size by c. 25% (Jakubas, 2004). *Neogobius melanostomus* may also benefit *P. auritus* in the Great Lakes, where predation on *N. melanostomus* reduces cormorant parasites. *Neogobius melanostomus* is a primary component of *P. auritus* diets at several sites in the Great Lakes (Somers *et al.*, 2003; Johnson *et al.*, 2006, 2010). At two sites in eastern Lake Ontario, for example, *N. melanostomus* was the dominant prey (79.4% by number overall, 81.1, 53.1 and 86.4 % by number during the pre-chick, chick and post-chick phases, respectively) of foraging adult *P. auritus* in the second season after *N. melanostomus* appeared (Johnson *et al.*, 2010). *Neogobius melanostomus* may indirectly alleviate predation pressure from *P. auritus* on *P. flavescens* and *M. dolomieu*, as annual bird consumption of these species declined during the post-*N. melanostomus* period (Johnson *et al.*, 2010). Conversely, *N. melanostomus* could subsidize top-down effects on native fishes in the long run if *P. auritus* populations increase. *Contracaecum* spp., a genus of cormorant parasites, have not been reported in *N. melanostomus*; thus, increased consumption of *N. melanostomus* could lead to diminished parasitism rates (Robinson *et al.*, 2009). Male *P. auritus* had greater than twice the *Contracaecum* spp. than females, probably because males fed in pelagic

waters (which contain *A. pseudoharengus*, a known *Contracaecum* spp. intermediate host) while females preferred benthic littoral areas in which *N. melanostomus* was the most accessible prey (Robinson *et al.*, 2009).

Neogobius melanostomus predation has contributed to community shifts at lower trophic levels as well. Invertebrates in invaded Lake Erie tributaries had reduced Shannon diversity, Ephemeroptera, Plecoptera and Trichoptera (EPT) richness and EPT:chironomid ratios, and increased macroinvertebrate density relative to streams without *N. melanostomus*, although there was no difference in non-Diptera density or total taxa richness (Krakowiak & Pennuto, 2008). In Green Bay, Lake Michigan, several macroinvertebrate species (dreissenids, isopods, amphipods, trichopterans and gastropods) significantly decreased in abundance from 2003 (when *N. melanostomus* was absent) to 2006 (when *N. melanostomus* was present) (Lederer *et al.*, 2008). In similar fashion, a 94% decline in quagga mussels *Dreissena bugensis* and a 85% decline in amphipods (*Gammarus fasciatus* and *Echinogammarus ischnus*) correlated with an increase in *N. melanostomus* density from 6.5 to 14 m⁻² from 2001 to 2004 in eastern Lake Erie (Barton *et al.*, 2005).

Neogobius melanostomus consumption of dreissenids may lead to localized declines in dreissenid abundance, but consumption rates are not high enough to effect dreissenid populations on a system-wide scale. In central Lake Erie (an area where *N. melanostomus* is abundant), it is estimated that *N. melanostomus* annually consumed an annual average of 6×10^3 t of dreissenids 1995–2002 (Bunnell *et al.*, 2005; Madenjian *et al.*, 2010). Biomass estimates for dreissenids were 100 times greater than the biomass consumed by *N. melanostomus* over that period; thus, it is unlikely that *N. melanostomus* affects standing dreissenid populations over large geographical scales (Bunnell *et al.*, 2005). In fact, lake whitefish *Coregonus clupeaformis* (Mitchill 1818) consumed far more dreissenids (109 and 820×10^3 t in Lakes Michigan and Huron respectively) than *N. melanostomus* (Madenjian *et al.*, 2010).

Nevertheless, the strong trophic link between *N. melanostomus* and mussels (dreissenids in the Great Lakes and other species in the Baltic Sea) facilitates the transfer of previously unavailable energy up to higher trophic levels. *Neogobius melanostomus* may be the only common forage fish to rely heavily on exploiting mussels as prey in both the Laurentian Great Lakes and the Baltic Sea. This review found that mussels comprise 65.3–88.9% of *N. melanostomus* diets in the Baltic Sea (Table III), where *N. melanostomus* serve as an important food source for *G. morhua* and *P. fluviatilis* (22.4 and 69.2% of diet by mass on average, respectively) (Almqvist *et al.*, 2010). Although mussels are prevalent in the diet of native *P. flesus*, neither *G. morhua* nor *P. fluviatilis* feed heavily on *P. flesus*. Invasive *N. melanostomus* is the only mussel-feeding fish to contribute substantially to *G. morhua* and *P. fluviatilis* diets, forming a new energetic pathway from mussels to piscivores at top trophic levels (Almqvist *et al.*, 2010). Similarly, benthic-oriented piscivorous fishes show substantial reliance on *N. melanostomus* as prey in the Laurentian Great Lakes (Table IV) where dreissenids constitute the majority of adult *N. melanostomus* diets (Table III). Thus, *N. melanostomus* facilitates the transfer of previously unavailable energy (from dreissenids) up to higher trophic levels (Johnson *et al.*, 2005a). While predators vary in their reliance on *N. melanostomus* as forage, its invasion has undoubtedly altered the flow of energy through Laurentian Great Lakes and Baltic Sea food webs.

Dreissenids may also facilitate the continued spread of *N. melanostomus* throughout North America. Dreissenids preceded *N. melanostomus* in most of its range in the Laurentian Great Lakes, leading several authors to hypothesize that *N. melanostomus* would continue to spread to areas with high dreissenid abundance (Jude *et al.*, 1995; Ray & Corkum, 1997; Ricciardi & MacIsaac, 2000). In addition to providing abundant forage, dreissenids also facilitated the invasion of another *N. melanostomus* prey item, the Ponto-Caspian amphipod *E. ischnus* (Stewart *et al.*, 1998; Ricciardi & MacIsaac, 2000). *Neogobius melanostomus* do not promote the replacement of native *G. fasciatus* by *E. ischnus* as once hypothesized, but both species are important forage for *N. melanostomus* (Kestrup & Ricciardi, 2009). The presence of dreissenids is not a necessary condition for *N. melanostomus* invasion: the species has established large populations in many areas devoid of dreissenids (Carman *et al.*, 2006; Kornis & Vander Zanden, 2010; Poos *et al.*, 2010). Nonetheless, since *N. melanostomus* co-evolved with dreissenids and prey on them in its native range (Jude *et al.*, 1995), it is logical to conclude that dreissenid presence facilitates *N. melanostomus* invasion.

The trophic links between *N. melanostomus*, dreissenids and *E. ischnus* support invasion meltdown theory, which suggests that introduced species expedite one another's establishment, spread and effects (Simberloff & Von Holle, 1999; Simberloff, 2006). Approximately 70% of species introduced to the Great Lakes between 1985 and 2000 were from the Ponto-Caspian region (Reid & Orlova, 2002), leading several authors to cite the Great Lakes as an example of invasion meltdown (Simberloff & Von Holle, 1999; Ricciardi, 2001; Vanderploeg *et al.*, 2002). Ponto-Caspian species have been similarly successful in the Baltic Sea, where 16 Ponto-Caspian species had established by 2000 (Reid & Orlova, 2002). Ponto-Caspian species may also be especially successful invaders because of exposure to a wide variety of environmental conditions (particularly salinity) during periods of isolation and connection between the Black, Caspian and Mediterranean Seas over evolutionary time (Reid & Orlova, 2002). As a result, wide environmental tolerance, euryhalinity and high phenotypic variability characterize many Ponto-Caspian species (Reid & Orlova, 2002). These characteristics, combined with facilitative interactions between species, heavy traffic from transoceanic vessels (Ricciardi & MacIsaac, 2000) and environmental similarities between the Ponto-Caspian, Baltic and Great Lakes regions, explain the high number of successful Ponto-Caspian introductions.

CONTAMINANTS AND CYCLING

Great Lakes *N. melanostomus* may facilitate bioaccumulation of toxic substances [mercury, polychlorinated biphenyls (PCB) and polychlorinated naphthalenes (PCN)] to upper levels of the food web. Models suggest PCB levels in age 3 year *N. melanostomus* range between fish that are safe to eat a few times a month (0.25 mg kg^{-1}) and the 'do not eat' threshold established by the U.S. Environmental Protection Agency fish advisory standards (Ng & Gray, 2009). Nonetheless, *N. melanostomus*'s potential role as a contaminant vector has been the subject of much debate, with a number of studies suggesting that *N. melanostomus* increases bioaccumulation of sediment-related toxins in predatory fishes (Kwon *et al.*, 2006; Hogan *et al.*, 2007; Ng *et al.*, 2008; Azim *et al.*, 2011), while other studies conclude the opposite (Hanari *et al.*, 2004; Fernie *et al.*, 2008).

Transfer of contaminants to upper trophic levels are related to *N. melanostomus* diets, which are heavily dominated by dreissenids in the Great Lakes. Since *N. melanostomus* is important forage for many piscivores in the Laurentian Great Lakes (Table IV), they link dreissenids to species like *M. dolomieu* and *P. flavescens* (Johnson *et al.*, 2005a; Hogan *et al.*, 2007). Sediment-related contaminants were assumed to be confined to dreissenids and other members of the benthos prior to *N. melanostomus* invasion; bioaccumulation models of toxicants suggest that contaminants are now recycled via *N. melanostomus*'s consumption of lipid-rich fish eggs and mussels (Ng *et al.*, 2008). A pre and post-*N. melanostomus* study found that *M. dolomieu* continued to accumulate mercury (Hg) at pre-invasion levels (1993) in 2003 despite declines in sediment Hg concentrations over that decade, presumably due to a *N. melanostomus*-rich diet (Hogan *et al.*, 2007). Similarly, total Hg concentrations in four Lake Erie species (*S. vitreus*, *P. flavescens*, *M. dolomieu* and *M. chrysops*) increased after *N. melanostomus* became abundant in the mid-1990s despite a significant decrease of Hg levels in sediment (Azim *et al.*, 2011). These findings are pertinent to fish consumption advisories for anglers, as Hg concentrations were highest in skinless boneless fillets and rate of Hg concentration increase was greatest in *S. vitreus*, a popular eating species (Azim *et al.*, 2011).

Evidence also suggests increased PCB accumulation related to the *N. melanostomus* invasion. One study found PCB contamination increased three to five-fold at each successive trophic level (*e.g.* dreissenids → *N. melanostomus*; *N. melanostomus* → *M. dolomieu*) and that PCB levels in *M. dolomieu* and *N. melanostomus* were relatively constant across a gradient of PCB sediment concentration, concluding that exotic species (dreissenids and *N. melanostomus*) contribute to contaminant recycling (Kwon *et al.*, 2006). An integrated bioenergetics and bioaccumulation model also indicated that *N. melanostomus* had higher mean PCB concentrations than *C. bairdii* (Ng & Gray, 2009), a benthic fish species being widely displaced by *N. melanostomus* in the Great Lakes (Lauer *et al.*, 2004). Contaminants have also been shown to affect *N. melanostomus*: greater fin loss, elevated concentration of copper and cadmium in liver tissue, greater proportion of females and intersex gonads in males were observed in *N. melanostomus* from contaminated sites relative to clean ones in Hamilton Harbour (Marentette *et al.*, 2009). Marentette *et al.* (2009) also demonstrated *N. melanostomus* can be abundant in polluted habitats, potentially attracting predators and thus facilitating mobilization of contaminants.

Despite the above evidence, *N. melanostomus* may not always contribute to the biomagnification of toxicants in the Great Lakes benthic food web. Hogan *et al.* (2007) observed that PCB contamination was higher in *M. dolomieu* before the invasion of *N. melanostomus*, suggesting that *N. melanostomus* contributed to bioaccumulation of Hg, but not PCB. Another study focused on PCNs, toxic contaminants quite similar to PCBs, and found that biomagnification of PCNs was not evident in *N. melanostomus* (Hanari *et al.*, 2004). Researchers in Lake Erie estimated that *N. melanostomus* contributed 2–6% and 8–19% increases in PCB transfer to pelagic and benthic piscivores, respectively, but *N. melanostomus* did not contribute as much to changes in fish PCB concentrations as increased PCB concentrations in sediments due to wind-related water turbulence (Morrison *et al.*, 2000). Finally, PCB and 1,1-dichloro-2,2-bis[*p*-chlorophenyl]ethylene (*p*, *p'*-DDE; a breakdown product of the formerly common but now banned pesticide DDT) concentrations remained stable in Lake Erie watersnakes despite dramatic changes in watersnake diet (25% amphibians

and 75% fishes that do not eat *D. polymorpha* compared to 95% *N. melanostomus* after the invasion of *N. melanostomus*) (Ferne et al., 2008). *Neogobius melanostomus* was also predicted to influence phosphorus cycling in Lake Erie through excretion and consumption of dreissenids, but a bioenergetics model suggested that *N. melanostomus* probably did not attain a sufficiently high biomass density to influence phosphorous cycling (Bunnell et al., 2005). On the basis of these findings, *N. melanostomus* probably results in increased heavy metal (Hg) recycling compared to historical levels, but recycling and trophic-level bioaccumulation of PCBs and PCNs is widely variable and more dependent ambient levels of sediment contamination.

AVIAN BOTULISM

Recent outbreaks of botulism amongst fish-eating birds spurred research into the driving factors, and *N. melanostomus* appears to be a key contributor. Fishes have served as vectors for botulism in birds since well before the invasion of *N. melanostomus*, including three outbreaks from 1963 to 1964 leading to an estimated 12 000 seabird mortalities (Fay et al., 1965) and several smaller outbreaks during the 1970s and 1980s (Brand et al., 1983). Over the past decade, however, botulism-related bird mortalities have become an annual problem (Yule et al., 2006a; Lafrancois et al., 2011). Multiple species are affected: a recent study found that 21 of 25 examined bird species had at least one individual test positive for *Clostridium botulinum* toxin type E, with a range of 25–100% of examined individuals testing positive (Hannett et al., 2011). *Neogobius melanostomus* is a probable vector because it spends almost 100% of its time near the lake bottom (Jude et al., 1992; Charlebois et al., 1997) where *C. botulinum* is more likely to be present (Yule et al., 2006a) and are especially abundant in shallow waters where most seabirds feed. *Neogobius melanostomus* is also sensitive to low levels of chronic exposure to botulism toxin (Yule et al., 2006b) and is very abundant in areas where bird mortalities occur, with densities reported to surpass 100 fish m⁻² in some areas (Corkum et al., 1998; Steinhart et al., 2004a). Fish-eating birds favour prey whose swimming behaviour makes them easier to capture (Barr, 1973) and infected *N. melanostomus* exhibit hyperpigmentation and erratic swimming during the last few hours before death, making infected fish stand out as easy prey targets (Yule et al., 2006a). Botulism is probably not a threat to humans consuming fishes because fillet tissues in three commercially relevant species [rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), *S. vitreus* and *P. flavescens*] consistently tested negative for *C. botulinum* neurotoxin (Yule et al., 2006c). Non-fillet tissues (organs), however, had much higher rates of positive testing, especially in *N. melanostomus*, where 92% of fish infected with botulism toxin had non-fillet tissues that tested positive (Yule et al., 2006c).

The combination of *N. melanostomus* abundance at shallow depths, vulnerability to low-level neurotoxin exposure, erratic swimming behaviour when infected and higher infection rates compared to other species strongly suggest that *N. melanostomus* is a primary vector for botulism neurotoxin to fish-eating birds. Affected birds are often found with *N. melanostomus* in their guts (Hannett et al., 2011). Nonetheless, *A. grunniens* has also been observed to have high incidence of *C. botulinum* toxin type E, indicating that *N. melanostomus* is not the only source of avian botulism (Hannett et al., 2011). Another study examining trends in avian

botulism in Lake Michigan from 1963 to 2008 found that botulism outbreaks were cyclical and correlated with low water levels and high mean surface water temperature relative to average values (Lafrancois *et al.*, 2011). Thus, while *N. melanostomus* may be the primary transmitter of botulism to fish-eating birds, water conditions are also a primary driver (Lafrancois *et al.*, 2011).

MANAGEMENT

Neogobius melanostomus is too abundant and widespread in large systems such as the Laurentian Great Lakes and the Baltic Sea for eradication efforts to succeed. It may be possible to reduce *N. melanostomus* densities locally, but this would probably require a large, sustained effort on the scale of a commercial fishery. Thus, management efforts have focused on prevention campaigns towards aquatic invaders in general as well as early detection and eradication efforts in smaller systems. Bait and boating regulations in place in some U.S. states and Canadian provinces already make it illegal to transport *N. melanostomus* (and other species); similar regulations, if not in place, should be enacted in other regions to prevent human-mediated spread. In the Chicago Sanitary and Ship canal, an electric barrier was constructed in part to prevent the spread of *N. melanostomus* into the Mississippi River catchment (Steingraeber & Thiel, 2000). While *N. melanostomus* crossed the barrier site prior to its activation, electric barriers effectively prevent passage by *N. melanostomus* and other fishes (Steingraeber & Thiel, 2000).

Ballast water regulations for vessels entering the Great Lakes may prevent some future species invasions as well as additional *N. melanostomus* introductions. Current ballast regulations, mandated by the U.S. in 1993, require vessels declaring ballast to exchange water in mid-ocean prior to entering the Great Lakes, hoping high salinity will kill most freshwater species (Costello *et al.*, 2007). Such regulations are considered a temporary solution while other technologies are researched (Endresen *et al.*, 2004). Mid-ocean ballast water exchange (BWE) is not perfect, as euryhaline species may survive such conditions, although laboratory experiments suggest that BWE would dramatically reduce *N. melanostomus* survivorship in ballast tanks (Ellis & MacIsaac, 2009). Nonetheless, BWE regulations do not appear to have slowed the rate of species introduction in the Great Lakes (Vander Zanden *et al.*, 2010) and several empirical studies demonstrate that BWE is not 100% effective at eliminating freshwater species (Ricciardi & MacIsaac, 2008). The BWE regulations also do not apply to no-ballast-on-board (NOBOB) ships; most ships entering the Great Lakes are classified as NOBOB, and such vessels typically carry 46 t of residual ballast water and 15 t of sediment (Duggan *et al.*, 2005). Continued improvement to ballast regulation appears necessary to bolster defence against further Great Lakes introductions.

Eradication or control of *N. melanostomus* populations may be possible in smaller systems if action is taken soon after detection of the species. *Neogobius melanostomus* is susceptible to piscicides such as rotenone, but such toxicants do not discriminate between *N. melanostomus* and native species and thus are not ideal (Schreier *et al.*, 2008). In some cases, chemicals such as rotenone may be the only appropriate management tool and unwanted side effects (killing native fishes) may be acceptable if *N. melanostomus* is eradicated. In 2004, *N. melanostomus* was discovered in Pefferlaw Brook, a tributary to Lake Simcoe, Ontario. It was deemed a serious threat to

Simcoe's angling industry (Kurji *et al.*, 2006) and in 2005, rotenone was applied to a 5 km stretch of Pepperlaw Brook with the sole goal of eradicating *N. melanostomus* (Borwick & Brownson, 2006; Corkum *et al.*, 2008). Unfortunately, in this instance several *N. melanostomus* were captured a few months after treatment and despite an intense seining effort to remove the remaining *N. melanostomus*, individuals have since been captured in Lake Simcoe. This effort, the only example of an attempt to eradicate an *N. melanostomus* population, illustrates the potential of early detection and rapid response programmes.

Several control methods specific to *N. melanostomus* show promise, although none have been used in the field. *Neogobius melanostomus* is susceptible to bottom-release formulations of two piscicides (Bayluscide and antimycin); such treatments selectively target benthic fishes such as *N. melanostomus*, an improvement over chemicals that kill indiscriminately (Schreier *et al.*, 2008). Pheromones also have potential for use in selectively trapping and controlling *N. melanostomus* (Corkum *et al.*, 2008). Pheromone traps have not been field tested and would probably require greater effort than chemical treatments, but would also be highly specific to *N. melanostomus* and eliminate human health concerns associated with chemicals. Sustained, baited trapping has successfully controlled an invasive rusty crayfish *Orconectes rusticus* population in a small temperate lake (Hein *et al.*, 2006); since *N. melanostomus* is susceptible to the same trapping method (Kornis & Vander Zanden, 2010), a similar sustained effort might have success in a small, bounded ecosystem. In larger systems, commercial exploitation of *N. melanostomus* might reduce local abundance. *Neogobius melanostomus* is commercially harvested in its native range, where they are canned for human consumption (Jude *et al.*, 1992). Fishermen in the Baltic Sea readily eat *N. melanostomus* when captured (Ojaveer, 2006), although they are typically considered by-catch as markets are lacking in the Baltic Sea area (Sapota, 2004). In North America, *N. melanostomus* could potentially contribute to fish meal and oil markets, but the viability of a commercial fishery in the Laurentian Great Lakes has not been explored.

FUTURE RESEARCH NEEDS

Additional research is needed in several areas pertaining to *N. melanostomus* (Table V). As mentioned above, *N. melanostomus*-specific control methods need to be field tested to determine their viability for use in management. Continued research is needed to better understand ecosystem-level effects, including research into energy flow pathways underlying important fisheries in *N. melanostomus* invaded systems (Bunnell *et al.*, 2005; Johnson *et al.*, 2005a; Campbell *et al.*, 2009). As *N. melanostomus* continues to expand its range in the Mississippi River catchment, research is needed to predict how *N. melanostomus* will affect this system to help determine what preventative actions should be taken. Broader assessment of the suitability of sub-optimal habitats (marshes, soft substrata and oceanic salinities) is also needed for *N. melanostomus*. Current research indicates that *N. melanostomus* can live in such environments, but it is not known whether *N. melanostomus* pose a legitimate threat to these systems; as populations grow, *N. melanostomus* may increase its utilization of sub-optimal habitat. Over the next century, other Ponto-Caspian gobiids (*N. fluviatilis*, *B. gymnotrachelus* and *P. kessleri*) may invade the Great Lakes; research is

TABLE V. *Neogobius melanostomus* research needs based on issues raised by publications

Range expansion	Ecological & Economic Effects	Management	Reproduction	Miscellaneous
Evaluate how climate change will affect distribution	Determine long-term population level effects of egg predation on fish recruitment	Field test efficacy and side effects of bottom-release piscicides	Estimate survivorship of reproductive males post spawning	Describe winter behaviour and determine factors important for overwinter survival
Evaluate reasons behind different spread rates within and between ecosystem types	Economic assessment of value gained and lost from <i>N. melanostomus</i> invasion	Field test efficacy of pheromone traps	Determine if alternate male spawning tactic is due to female mimicry or sneaker spawning	Evaluate how morphological characteristics vary amongst <i>N. melanostomus</i> populations
Determine dispersal mechanisms and environmental and biological factors limiting dispersal	Comparison of effects in stream and lake ecosystems	Assess usage of live <i>N. melanostomus</i> as bait by anglers	Description of territoriality during spawning across a range of densities	Compare life history characteristics from stream and lake ecosystems
Determine abundance capacity in stream and lake ecosystems	Describe effects on energy flow pathways in different ecosystems	Assess inclusion of <i>N. melanostomus</i> as by-catch in bait sold at bait shops		Evaluate interactions with other potential gobiid invaders
Predict range expansion in recently invaded systems (e.g. Mississippi River, north-eastern Baltic Sea)	Evaluate role in resource switching by piscivores in invaded range	Cost-benefit analysis of preventing invasion of Mississippi River via electric barrier		Determine consequences of parasitism on <i>N. melanostomus</i> behaviour
	Determine how parasite loads affect predators of <i>N. melanostomus</i>			Determine potential for <i>N. melanostomus</i> to transfer viral haemorrhagic septicaemia virus (VHSV) to predators

needed to better understand the contrasts between *N. melanostomus* and these species and how they may interact with one another [Jurajda *et al.* (2005) and Harka & Bíró (2007) provide data on gobiids in Eurasian rivers].

There is also a great need for economic assessments of the costs of *N. melanostomus* invasions and invasions in general. Invasive species often most dramatically affect indirect and non-use values; while reductions in direct-use values are easiest to determine, neglecting changes to indirect-use and non-use values may result in ignoring substantial losses of utility and making poorly informed management decisions (Choquenot *et al.*, 2004; Born *et al.*, 2005). There is no definitive study on the economic costs of *N. melanostomus* in the Great Lakes, largely because this species degrades indirect-use values that are moderately difficult to measure. The most direct economic effect of *N. melanostomus* is associated with recreational angling. Depending on the target species, *N. melanostomus* either deters anglers from fishing due to frequent capture as by-catch, or encourages anglers to fish due to perceived increases in the frequency of above-average-sized fish (M. S. Kornis, unpubl. data). Egg predation by *N. melanostomus* could potentially affect recruitment of recreationally important fishes (Steinhart *et al.*, 2004a, Fitzsimons *et al.*, 2009a) and has resulted in *M. dolomieu* fishing closures in Lake Erie during the spawning season. Although this probably represents an economic loss, it is difficult to quantify due to the lack of studies evaluating long-term population-level effects of *N. melanostomus* egg predation on bottom-spawning species. Thus, it is difficult to determine whether *N. melanostomus* provides a net loss or gain to the Great Lakes recreational fishery.

Ecological effects of *N. melanostomus* are decidedly negative, but economic assessment is needed to quantify the costs of these losses. *Neogobius melanostomus* deplete food forage for juveniles of desirable fish species (Diggins *et al.*, 2002; Carman *et al.*, 2006), extirpate native benthivorous fishes (Dubs & Corkum, 1996; Balshine *et al.*, 2005), reduce biodiversity (Krakowiak & Pennuto, 2008), threaten imperilled species (Poos *et al.*, 2010), transfer biocontaminants such as mercury to fishes consumed by humans (Hogan *et al.*, 2007) and increase incidences of avian botulism (Yule *et al.*, 2006a). Benefits, including increased growth rates of some game fishes (Steinhart *et al.*, 2004b) and an endangered watersnake (King *et al.*, 2006), as well as potential amelioration of early mortality syndrome in *S. namaycush* (Jaroszewska *et al.*, 2009) should be considered as well, although costs probably outweigh benefits. *Neogobius melanostomus*-related changes in recreational and commercial fishing, human health and existence values could be evaluated through non-market valuation techniques such as contingent valuation surveys, which measure willingness to pay for non-market goods or services or travel-cost techniques, which examine a consumer's willingness to pay for travel to areas with and without a certain quality (in this case *N. melanostomus*).

CONCLUSIONS

Neogobius melanostomus is increasingly recognized as a globally significant invasive species. Several factors provide cause for concern. First, *N. melanostomus* often plays an important role in the food webs of invaded ecosystems; it is highly aggressive and often becomes the dominant fish species in nearshore benthic habitats. As a result, it frequently exerts strong predatory and competitive effects on native fishes

and invertebrates. In addition, *N. melanostomus* is often a dreissenid specialist, with mussels comprising *c.* 27 and 63% of *N. melanostomus* diets for <70 and >70 mm L_T classes respectively, in the Great Lakes (Table III). While *N. melanostomus* will invade areas without dreissenids, the spread and effect of *N. melanostomus* can be facilitated by the presence of invasive dreissenids (Dubs & Corkum, 1996; Ricciardi & MacIsaac, 2000). Dreissenids are renowned for being among the world's most aggressive and harmful aquatic invasive species. As a result of this food web link, *N. melanostomus* invasion may have the effect of unlocking a portion of the benthic production that is sequestered in dreissenid biomass. *Neogobius melanostomus* has become an important prey item for numerous native and non-native species (Table IV), thereby allowing this production (and in some cases contaminants) to be channelled up the food web to a variety of consumers.

Neogobius melanostomus is capable of inhabiting a wide range of temperate freshwater and brackish-water ecosystem types, including large lakes and small and large rivers. It has maintained a rapid rate of spread, reflecting a combination of several transport vectors: long-range ballast water transport, regional-scale transport by humans (bait release and intentional introductions) and natural dispersal through inter-connected catchments. In the Baltic Sea, *N. melanostomus* has established populations at several locations (off the coast of Karlskrona, Visby and Göteborg, Sweden, the Finnish Archipelago Sea and Gulf of Finland, the coast of southern Denmark and the Gulf of Riga, Estonia) over the past decade. Coastal areas with high salinity are not immune to invasion (Göteborg, Sweden, is on the coast of the Kattegat linking the Baltic and North Seas), but thus far range in areas like Göteborg have been limited to low-saline habitats of inner harbours, suggesting introduction by ship, not dispersal. *Neogobius melanostomus* will probably continue to expand its range along coastal habitats in the Baltic Sea until its distribution is limited by salinity. Isolated occurrences elsewhere in Europe (*e.g.* the Lek River, Netherlands, the Scheldt River, Belgium, and the Moscow River, Russia) provide additional source populations for natural and human-assisted dispersal to other inland waters. *Neogobius melanostomus* could also invade coastal salt marshes and estuaries, where salinities often mirror those of the Baltic Sea and *Mytilus* spp. are a prevalent potential food source (Stepien & Tumeo, 2006).

Neogobius melanostomus invasion of nearshore habitats and coastal tributaries of the Laurentian Great Lakes continues. It is expected that its range will expand to include virtually all littoral hard substrata of the Laurentian Great Lakes, perhaps with the exception of northern sections of Lake Superior and Lake Huron, where they will be limited by cold temperatures. Upstream expansion into Great Lakes tributaries will be hindered by the presence of dams, but *N. melanostomus* can make its way over dams with the assistance of humans and will continue to move upstream within the Great Lakes basin. They are already present in the Illinois River, a Mississippi River tributary; since *N. melanostomus* readily disperse downstream in the presence of dams, possibly through larval drift, they will probably invade the Mississippi River and continue downstream to its delta. *Neogobius melanostomus* will gradually spread upstream through portions of the Mississippi River basin as well. As in the Great Lakes basin, dams will serve as barriers to upstream movement, but will occasionally be overcome with human assistance.

In the absence of concerted international effort to limited global transport of live organisms in ballast water, entirely new regions of the world can be expected to be

invaded by *N. melanostomus* in the coming century. They can clearly survive long trips in the ballast water of transoceanic vessels (Jude *et al.*, 1995; Hensler *et al.*, 2008), and could establish at any port receiving ballast water from a vessel that took on ballast in *N. melanostomus*-occupied waters. Oceanic ballast water exchange may help limit further spread of *N. melanostomus* (Ellis & MacIsaac, 2009), but many vessels are exempt from ballast water exchange regulations (Duggan *et al.*, 2005). Newly established populations would be able to disperse upstream into adjacent river systems and could further spread due to human transport (*e.g.* bait buckets and live wells).

The ultimate distribution and effect of *N. melanostomus* will be influenced by anthropogenic climate change. Studies discussing climate change and invasive species have posited that climate change could facilitate the spread of certain species and amplify their ecological effects (Pyke *et al.*, 2008; Rahel & Olden, 2008). It is believed that this will be the case for *N. melanostomus*. A doubling of atmospheric CO₂ is expected to cause a 2.4–7.7° C increase in summer water temperature in the Laurentian Great Lakes watershed [90% of predicted increase in air temperatures reported by Mortsch & Quinn (1996), concurrent with air and water temperature correlations from Stefan & Preud'homme (1993)]. Increased water temperatures will allow the geographic range of *N. melanostomus* to shift northwards (*i.e.* Lake Superior and tributaries) and should benefit *N. melanostomus* throughout much of its invasive range, as temperatures will approach energetically optimal temperatures reported by Lee & Johnson (2005). Warmer water temperatures could lead to faster growth rates in *N. melanostomus*, which in turn could facilitate greater rates of contaminant bioaccumulation in *N. melanostomus* and its predators (Ng & Gray 2011). Alternatively, excessively warm water temperatures could limit the occurrence of *N. melanostomus* in certain tropical and subtropical regions (*i.e.* the south-eastern U.S.A.). Since fishes tolerate lower dissolved oxygen levels at cooler temperatures (Schurmann & Steffensen, 1997), warmer temperatures could also magnify the effects of hypoxia on *N. melanostomus*, which has been shown to limit growth rate potential in Lake Erie (Arend *et al.*, 2011). Ultimately, the global spread and influence of this species will depend on a complex array of interactions among biotic and environmental factors. Although there remain many uncertainties regarding its ultimate distribution and economic and ecological effects, *N. melanostomus* will be a species of growing management concern over the next century.

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