

# Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species

P. M. Kocovsky · J. A. Tallman · D. J. Jude ·  
D. M. Murphy · J. E. Brown · C. A. Stepien

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**Abstract** The Eurasian freshwater tubenose goby *Proterorhinus semilunaris* (formerly *Proterorhinus marmoratus*) invaded the Laurentian Great Lakes in the 1990s, presumably via ballast water from trans-oceanic cargo ships. Tubenose gobies spread throughout Lake St. Clair, its tributaries, and the Detroit River system, and also are present in the Duluth-Superior harbor of Lake Superior. Using seines and bottom trawls, we collected 113 tubenose gobies between July 2007 and August 2009 at several locations in western Lake Erie. The number and range of sizes of specimens collected suggest that tubenose gobies have become established and self-sustaining in the

western basin of Lake Erie. Tubenose gobies reached maximum densities in sheltered areas with abundant macrophyte growth, which also is their common habitat in native northern Black Sea populations. The diet of tubenose gobies was almost exclusively invertebrates, suggesting dietary overlap with other benthic fishes, such as darters (*Etheostoma* spp. and *Percina* sp.), madtoms (*Noturus* spp.), and sculpins (*Cottus* spp.). A single mitochondrial DNA haplotype was identified, which is the most common haplotype found in the original colonization area in the Lake St. Clair region, suggesting a founder effect. Tubenose gobies, like round gobies *Neogobius melanostomus*, have early life stages that drift owing to vertical migration, which probably allowed them to spread from areas of colonization. The Lake St. Clair-Lake Erie corridor appears to have served as an avenue for them to spread to the western basin of Lake Erie, and abundance of shallow macrophyte-rich habitats may be a key factor facilitating their further expansion within Lake Erie and the remainder of the Laurentian Great Lakes.

**Keywords** Corridor · mtDNA sequence · PCA · Substrate · Vegetation

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P. M. Kocovsky (✉)  
U.S. Geological Survey, Lake Erie Biological Station,  
6100 Columbus Avenue, Sandusky, OH 44870, USA  
e-mail: pkocovsky@usgs.gov

J. A. Tallman · D. J. Jude  
School of Natural Resources and Environment, University  
of Michigan, 440 Church Street, Ann Arbor,  
MI 48109-1515, USA

D. M. Murphy · J. E. Brown · C. A. Stepien  
Lake Erie Center and Department of Environmental  
Sciences, University of Toledo, 6200 Bayshore Dr,  
Toledo, OH 43616, USA

*Present Address:*

J. A. Tallman  
526 W Broadway St., Maumee, OH 43537, USA

## Introduction

The Laurentian Great Lakes (hereafter Great Lakes) have a long history of species invasions (Mills et al.

1993). Since the opening of the Welland canal in the mid 1900s to provide a shipping route around impassable Niagara Falls, which is between lakes Ontario, the downstream-most lake, and Erie, over 170 non-indigenous species have successfully established in the Great Lakes (Holeck et al. 2004). A large proportion of species invasions are attributed to ballast water introductions from transoceanic vessels (Mills et al. 1993; Holeck et al. 2004), although a few, such as sea lamprey *Petromyzon marinus* and white perch *Morone americana* likely arrived on their own by way of the numerous canal systems that interconnect waterways throughout the Great Lakes region (Mills et al. 1993). Many of these invasions have caused or contributed to reductions or extirpations of native populations (e.g., sea lamprey parasitism greatly reducing lake trout *Salvelinus namaycush* populations in Lake Erie). Because of similarity of conditions to the Great Lakes region, a number of successfully established invasive species have originated from the Ponto-Caspian region (Ricciardi and MacIsaac 2000).

The Ponto-Caspian-native freshwater tubenose goby *Proterorhinus semilunaris* was first sampled in the Great Lakes in the St. Clair River in 1990, where it was introduced via ballast water (Jude et al. 1992). The species is native to freshwater waterways in the northern Black Sea and was recently resurrected as a separate species from marine tubenose goby *P. marmoratus*, genetically diverging ~ 4.2–4.4 million years ago (mya) (Stepien and Tumeo 2006; Neilson and Stepien 2009). No *P. marmoratus* occur in the Great Lakes or in other areas of North America, and are native to marine Black Sea waters. Freshwater tubenose gobies were established throughout the Huron-Erie Corridor (HEC) by the year 2000 (Leslie et al. 2002) and four mitochondrial (mt) DNA cytochrome (cyt) *b* haplotypes have been described from this region, with type 4 being the most common (Neilson and Stepien 2009). Expansion of freshwater tubenose gobies into other lakes and habitats has been more gradual (Vanderploeg et al. 2002). In addition to being established throughout the HEC, freshwater tubenose gobies are captured commonly in Duluth/Superior harbor in Lake Superior (Dopazo et al. 2008), where only cyt *b* haplotype 4 has been identified (Neilson and Stepien 2009). Leslie et al. (2002) reported tubenose gobies on the north shore of western Lake Erie, but more recent sampling by Reid

and Mandrak (2008) produced no tubenose gobies at several north shore sites or around Pelee Island. Freshwater tubenose gobies in the Great Lakes typically are found in rocky substrates but also inhabit sandy areas and aquatic macrophytes (Jude and DeBoe 1996). Most past samples of tubenose gobies from the Great Lakes have been from shallow depths, typically less than 3 m, with a few individuals captured as deep as 5 m, but none captured deeper than 5 m (e.g., Dopazo et al. 2008; Jude and DeBoe 1996). Freshwater tubenose gobies from river systems in the northern Black Sea were most frequently found in slow-moving shallow areas with abundant macrophytes (C. Stepien, unpublished data). French and Jude (2001) reported that tubenose goby diets elsewhere in the Great Lakes included ephemeropterans, trichopterans, dipterans, crustaceans, and occasionally larval fishes (French and Jude 2001). This contrasts somewhat with diets in the Danube River in Bulgaria, which consisted primarily of chironomids, secondarily ostracods, Trichoptera, Ephemeroptera, and Copepoda (Adamek et al. 2007). In the Great Lakes tubenose goby diet overlaps seasonally with rainbow darters *Etheostoma caeruleum*, and northern madtoms *Noturus stigmosus* (French and Jude 2001).

Since their invasion, freshwater tubenose gobies mostly have remained within short distances of areas of original invasion (Vanderploeg et al. 2002), which typically are harbors that receive vessel traffic from throughout the Great Lakes and beyond. Since 2007 we have captured individual tubenose gobies in areas distant from known areas of introduction and in new habitats in western Lake Erie suggesting the species' range is expanding. Here we report on expansion of the range of tubenose gobies and their diet and habitat associations in western Lake Erie. We also discuss the genetic origins of invasive tubenose gobies in Lake Erie, potential for future expansion, mechanisms of expansion, and possible effects on native species.

## Methods

Sampling was conducted at numerous locations around several islands in western Lake Erie in 2007–2009 and in open waters of western Lake Erie in 2008 and 2009. Around the Bass Islands, Kelley's Island, and Catawba Island in 2008 (Fig. 1) most

sampling was conducted along 20-m lengths of shoreline using a 12-m long beach seine with a 6.5-mm bar mesh size and a large bag similar, but larger, than the one specially designed to catch gobies (Jude and DeBoe 1996). The width of hauls was 11 m. At a few sites on South Bass Island where large boulder deposits made seining evenly spaced 20-m transects impossible, we seined 120-m lengths of beach in several increments. When a boulder was too large to sample around, the seine was brought to shore and the catch counted and retained. Seining then resumed as close as possible on the opposite side of the boulder. For 120-m hauls, we measured the total distance seined to calculate catch per unit effort (number of fish/ha). We also used a 15-m bag seine with 6.5-mm-bar mesh and a 1.8-m bag to collect six samples each within a 24-h period at Alligator Bar on Gibraltar Island on 23 July 2008 and 30 July 2009. Each of the six seine hauls covered 671 m<sup>2</sup> in 2008 and 583 m<sup>2</sup> in 2009. Qualitative seine sampling was also conducted on Alligator Bar on 4 August 2009 and on 2 August 2009 in Terwilliger's Pond, a highly vegetated wetland connected via a large cement culvert to Lake Erie at Put-in-Bay, Ohio. All tubenose gobies captured by seining were euthanized in an overdose of MS-222, then preserved in 70% ethanol.

At each seine site visual estimates of percent coverage of macrophytes and six substrate types based on Wentworth categories (bedrock, boulder, cobble, gravel, sand, and silt) were recorded. A Principal Component Analysis (PCA) of substrate and macrophyte variables was conducted to determine gradients in these variables with which tubenose goby presence and density were correlated. The substrate and macrophyte coverage variables were transformed [ $\log_{10}(\text{variable} + 1)$ ] to account for zero values and to meet assumptions of PCA. Relationships between tubenose goby density and each principal component were examined using Pearson product-moment correlations. One-way ANOVA was conducted individually on each of the first two principal components to examine whether tubenose goby presence was associated with the gradients identified in the PCA. All analyses were done in SAS version 9.1.

In June and September 2008–2009 we sampled 25 open-water sites in Michigan and Ontario waters of western Lake Erie with a 7.9-m headrope bottom trawl with 2.5-cm (bar measure) mesh body and 5-mm opening cod end. Trawl tows were 10 min in duration

at approximately 2 kts and covered  $0.253 \pm 0.014$  (95% CI) ha. Suspected tubenose gobies were enumerated by site of capture and frozen in the field. Specimens were identified to species in the lab using a dichotomous key (Hubbs et al. 2004) and pectoral fins were removed and placed in 70% ethanol for genetic analysis. To further verify that captured individuals were freshwater tubenose gobies and to identify the possible origin(s) of their source population(s), the entire mitochondrial (mtDNA) cytochrome (cyt) *b* gene (1138 bp) was amplified via the polymerase chain reaction (PCR) and sequenced following the procedure outlined in Neilson and Stepien (2009).

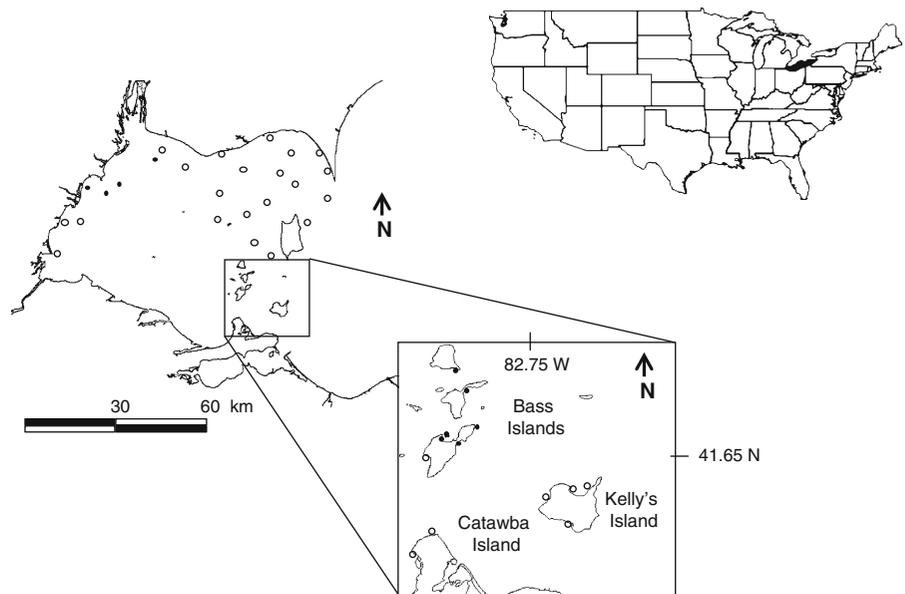
In the laboratory, tubenose gobies were weighed to the nearest 0.01 g, measured to the nearest mm, and stomachs were removed from selected individuals captured in seines. Stomach contents were weighed to the nearest 0.01 g, then individual taxa found in the stomachs were counted, and a visual estimate was made of each taxon's percent composition of the total. This allowed a calculation of the percentage each group composed of the total weight (see French and Jude 2001).

## Results

We collected 99 freshwater tubenose gobies in quantitative sampling; 90 were captured in seines around South, Middle, and North Bass Islands between 9 August 2007 and 30 July 2009, and 9 were captured in trawl samples in September 2008 (Table 1). An additional 14 individuals were captured in qualitative seine samples during 28 July–4 August 2009 at Alligator Bar ( $N = 11$ , range: 22–55 mm) and Terwilliger's Pond ( $N = 3$ , range: 39–51 mm). Individuals ranged in total length from 20 to 72 mm. Several seine samples taken along shorelines of Catawba Island and Kelley's Island (Fig. 1) produced no tubenose gobies. Densities of tubenose gobies captured in seines ranged from 7/ha on Alligator Bar to 225/ha on South Bass Island.

Tubenose gobies were typically captured in areas protected from wave and wind action where scattered or dense vegetation was present (Table 1). Schoolhouse Bay of Middle Bass Island (Fig. 1), where tubenose gobies were fairly abundant in a wide range of sizes, was characterized by unusually clear water and diverse bottom composition. The substrate transitioned

**Fig. 1** Sites sampled for tubenose gobies *Proterorhinus semilunaris* in western Lake Erie (shaded in map of the United States) in 2007–2009. Closed circles represent sites where tubenose gobies were captured; open circles are sites sampled where no tubenose gobies were captured



**Table 1** Capture locations, range of total lengths, and densities of freshwater tubenose gobies *Proterorhinus semilunaris* captured in western Lake Erie during 2007–2009

Location	Date	N	TL range (mm)	Density (N/ha)
South Bass Island—East Point	9 August 2007	1	32	50
Middle Bass Island—Schoolhouse Bay	27 July 2007	13	20–54	106
	3 August 2007	33	25–56	138
South Bass Island <sup>a</sup>	17 October 2007	27	45–72	225
North Bass Island—South Cove	23 October 2007	10 <sup>b</sup>	35–57	42
South Bass Island—Gibraltar Island, Alligator Bar	23 July 2008	3	32–42	9
Open waters of western Lake Erie—four sites	23 September 2008	9	37–58	4–16
South Bass Island—Gibraltar Island, Alligator Bar	30 July 2009	3	39–50	7

<sup>a</sup> East Point (two sites), near Perry's Monument (two sites), State Park (two sites), and Oak Point

<sup>b</sup> One specimen (64 mm TL) was also found dead on shore

from bedrock reef to cobble and then sand interspersed with rock. Freshwater tubenose gobies increased in abundance with increasing depth, reaching maximum densities in about 1.5 m of water in areas with 25 to 30% macrophyte cover and a diverse, mostly rock bottom with some sand and silt.

The northeastern tip of South Bass Island, which was seined twice in 2007, also is a small embayment sheltered from the scouring waves with very irregular, hard bottom areas. The greatest density of tubenose gobies was observed here when macrophyte cover was 50%. No tubenose gobies were collected on 4 November 2007 at this site, which then lacked macrophytes, leaving the area exposed and barren.

Perry's Monument swimming beach, where a single specimen (48 mm) was collected in 2001 (J. Hageman, personal communication, T. Stone Laboratory, Ohio State University, Put-in-Bay, Ohio), also is protected from strong winds and waves and had cobble, rip-rap, rocky substrate, and macrophytes. Alligator Bar on Gibraltar Island is a rocky reef, with a diversity of rocks, cobble, and gravel and 20% macrophyte cover. Three tubenose gobies were collected there during 2008 and three others (39–50 mm TL) in 2009, whereas an additional 11 (22–55 mm TL) were collected there during qualitative seining for other species on 4 August 2009. In similar annual sampling at this reef from 1995 to

2006, no tubenose gobies were collected (D. Jude, unpublished data). The southern tip of North Bass Island has a habitat type very similar to the other sheltered areas where tubenose gobies were captured.

Tubenose gobies generally were not found in areas dominated by cobble, windswept shores, or areas lacking a diversity of habitat, especially a lack of vegetation. This was demonstrated by sampling South Bass Island State Park as a control site (Fig. 1). Habitat features there included high water clarity, varied substrate of cobble and rock with sparse macrophytes, but was exposed to open water and large waves from prevailing winds from the west. Eight seine hauls at four locations produced no tubenose gobies. Similar habitat at two sites on the southern and western shores of Kelley's Island and two sites on Catawba Island yielded no tubenose gobies.

Gravel and bedrock percentages were zero at most seine sites. Because these zero values would have had a strong influence on the outcome of PCA we added proportions for silt and sand, gravel and cobble, and boulder and bedrock to create three mostly non-zero substrate variables representing small, moderate, and large substrates, respectively. Macrophyte cover was the fourth variable used in PCA. The first two principal components (PC) explained 89% of the variation in substrate and macrophyte cover (Table 2). The first PC reflected primarily a substrate size gradient, with silt/sand loading negatively and larger particles loading positively. The second PC reflected primarily a macrophyte gradient and secondarily a moderate-to large substrate-type gradient. Freshwater tubenose goby density was weakly negatively correlated with PC1 ( $r = -0.22$ ,  $P = 0.23$ ) but was positively correlated with PC2 ( $r = 0.47$ ,  $P = 0.008$ ). Thus, tubenose goby density was positively related to macrophyte cover. Scores on PC1 did not vary with presence of tubenose gobies (ANOVA,  $F_{1, 32} = 0.34$ ,  $P = 0.56$ ), whereas those on PC2 did

(ANOVA,  $F_{1, 31} = 8.0$ ,  $P = 0.008$ ). Thus, presence of tubenose gobies was related primarily to macrophyte cover.

We captured nine tubenose gobies (37–58 mm TL) at four of 25 open-water sites sampled in Michigan and Ontario waters of western Lake Erie (Fig. 1) during trawling in September 2008. Depths of capture ranged from 3 to 7 m, while densities ranged from 4 to 16 fish per ha (Table 1). Trawl samples contained comparatively large masses of rooted and attached aquatic macrophytes, up to a few kg in wet weight, and up to several kg of dreissenid mussels and shells, at all four sites where tubenose gobies were captured. Macrophytes were sparse or absent from trawl samples where tubenose gobies were not captured. Trawling of the same sites in June 2008 and in June and October 2009 produced no tubenose gobies. Trawling in 6 m of water near South Bass Island in 2008 produced no tubenose gobies (A. Turnbull, personal communication, Stone Laboratory, Ohio State University, Put-in-Bay, Ohio).

Analysis of mtDNA *cyt b* from fin clips from 10 specimens captured in trawls confirmed they were freshwater tubenose gobies, i.e., *Proterorhinus semilunaris*. All 10 had the most common haplotype characteristic of 70% of those sequenced from the Clinton River near Lake St. Clair (haplotype 4 of Neilson and Stepien 2009; GenBank Accession EU444607).

Diets by weight of tubenose gobies ( $N = 48$ ) captured around the Bass Islands were composed mostly of invertebrates (Table 3). Chironomids dominated the diets at three of the four sites (on North and South Bass Islands), while amphipods were more abundant in diets of fish from Middle Bass Island. South Bass Island tubenose gobies also ate a more diverse range of food items than tubenose gobies from the other sites. Overall, chironomid larvae were the most common group consumed (57% by weight), followed by unidentified material (17%), amphipods

**Table 2** Summary of Principal Component Analysis results for substrate and vegetation variables in western Lake Erie at sites sampled for tubenose gobies during 2007–2009

PC	Eigenvalue	% Variation explained	Loadings on Eigenvectors			
			Silt/sand	Gravel/cobble	Boulder/bedrock	Macrophytes
1	0.018	67	-0.731642	0.598542	0.248418	0.211509
2	0.0059	22	0.020271	-0.452743	0.560124	0.693451

**Table 3** Summary of diet of tubenose gobies *Proterorhinus semilunaris* (27–72 mm) collected 3 August–23 October 2007 around the Bass Islands in western Lake Erie. Provided are

sample sizes (N) and the mean number (n) and weight (g) of food items eaten at the various sites. Miscellaneous included: Trichoptera, Coleoptera, *Hydracarina*, Odonata, and *Bosmina*

Location	N	% with food	Chironomid									
			Larvae		Pupae		Amphipod		Unidentified		Miscellaneous	
			n	Weight	n	Weight	n	Weight	n	Weight	n	Weight
North Bass Island—South Cove	10	80	1.2	0.002	0.6	0.001	0	0	0	0	0	0
South Bass Island—East Point	1	100	4	0.002	0	0	0	0	0	0	3	0.008
South Bass Island—East Point	27	100	44	0.036	2.2	0.003	1.4	0.008	0	0	0.6	0.003
Middle Bass Island—Schoolhouse Bay	21	57	0	0	0.2	0.001	0.3	0.003	0.9	0.015	0	0

(14%—*Gammarus* and *Echiogammarus* spp.), miscellaneous (6%—Trichoptera, Coleoptera, *Hydracarina*, Odonata, *Bosmina*), and chironomid pupae (6%).

## Discussion

The expansion of tubenose goby throughout the Laurentian Great Lakes to date has been much slower than that of round gobies *Neogobius melanostomus* (Vanderploeg et al. 2002), although both colonizations appeared to have substantial genetic variability, according to mt cyt *b* data (Stepien et al. 2005; Brown and Stepien 2009). Although the original HEC population of tubenose goby had an appreciable amount of genetic diversity (as high as or higher than native population sites; see Stepien et al. 2005), tubenose gobies are markedly less abundant in these Great Lakes areas in comparison to round gobies. It may be that they experienced a longer population growth “lag effect” and possibly Allee effect. It thus may have taken more time for the population to become established and grow in the HEC, and likewise took more time for freshwater tubenose gobies to spread to Lake Erie. The tubenose goby also tends not to be as abundant as the round goby in their native habitats (C. Stepien, personal observation).

Documented expansions of tubenose goby to date have been saltatory, e.g., in commercial shipping ports and harbors, and once tubenose gobies have become established, expansions beyond those areas have not occurred. An example of this is the St. Louis harbor population in Lake Superior, which was 100% of cyt *b* haplotype 4 (Neilson and Stepien 2009), and, thus, had lower genetic variability than did the

original population in the HEC. This outcome likely is due to a founder effect. A similar saltatory pattern of establishment in connection with shipping ports also has been reported throughout the Danube River basin in Europe (Wiesner 2005). Our capture of a wide range of sizes (and probably ages) of tubenose gobies, comparable to the size range in other invaded habitats (e.g., Danube River, Hungary, Erös et al. 2005), in open waters of western Lake Erie and at the Bass Islands, over 50 km from the mouth of the Detroit River where tubenose gobies are established, indicate that self-sustaining populations of tubenose gobies have become established around the Bass Islands and that an expansion by means other than new ballast water introductions is underway in western Lake Erie. Furthermore, our capture of a few individuals at 7 m represents an expansion of the range of depths at which tubenose gobies have been captured. Below we discuss potential mechanisms of tubenose goby expansion in western Lake Erie and the implications for native species if expansion of tubenose goby continues.

In general terms, invasions of new species can be anthropogenically assisted or unassisted. The presence of tubenose gobies around the Bass Islands and their discontinuous range in western Lake Erie suggests one possible vector for assisted establishment of tubenose gobies around the Bass Islands is by way of a bait bucket introduction. This was the mechanism for transfer of round gobies to the Flint and Shiawassee Rivers in the early 1990s (Carman et al. 2006). There are no major shipping ports on North or Middle Bass Islands, and most shipping traffic to South Bass Island originates from areas where tubenose gobies are not present (e.g., Sandusky Bay, Catawba Island, and Marblehead Peninsula).

Hence, we believe the arrival of tubenose gobies at the Bass Islands via ballast water was unlikely.

A bait bucket introduction, in which a small number of individuals was released, cannot be ruled out. Tubenose gobies are not a marketed species in the baitfish industry, and preliminary results of sampling commercially available baitfish in southern Ontario revealed no tubenose gobies (A. Drake, University of Toronto, personal communication). There are no known cases of tubenose gobies being found in baitfish samples in the US (T. Gabriel, Ohio Sea Grant, personal communication), but there has also not been a directed study in U.S. areas as there has been in Ontario. Steps have been taken to reduce the risk of spread of tubenose gobies by way of the baitfish industry; in the St. Louis River estuary in Lake Superior, where tubenose gobies are established, baitfish harvest has been banned. These studies and regulatory efforts suggest low potential for an unintentional bait bucket introduction, although an intentional release also cannot be excluded.

Alternate 'unassisted' mechanisms for expansion include drift associated with nighttime vertical migration of larvae (Zitek et al. 2004) and active movement. The rapid expansion of round gobies in the Great Lakes has been attributed in part to nighttime vertical migration of larvae (Hensler and Jude 2007), which likely facilitated their intake into ship ballast tanks, thus permitting more rapid expansion via the shipping industry. Such nighttime vertical migrations could also result in larval fish being transported passively to new habitats via currents, which are comparatively strong in the HEC and western Lake Erie. Nighttime drift of larval and juvenile freshwater tubenose gobies has been demonstrated in the Danube River system in Austria (Zitek et al. 2004), which has facilitated their expansion beyond commercial shipping ports. The high volume of water passing from the upper Great Lakes to Lake Erie through the Detroit-St. Clair river system creates a flow pathway for passive movement of tubenose gobies via drift, a mechanism confirmed for the observation of deepwater sculpin *Myoxocephalus thomsonii* larvae in Lake Erie (Roseman et al. 1998). The pattern of capture of tubenose gobies near the mouth of the Detroit River in open waters of western Lake Erie is consistent with the mechanism of current-driven drift. One site at which tubenose gobies were captured is proximal to Monroe,

Michigan, which is an international port. Tubenose gobies may have arrived there (and spread elsewhere) via ballast water release. Tubenose gobies may have also arrived via drift and perhaps through active movement to the Bass Islands and found suitable vegetated habitat that is largely lacking throughout open waters of the western basin of Lake Erie.

Our analysis of tubenose goby presence and density revealed a positive association with macrophyte cover. The propensity of tubenose gobies to associate with aquatic vegetation suggests that vegetation may provide a corridor for their future expansion throughout Lake Erie. Since the invasion of dreissenids, water clarity has increased in the HEC and throughout the western basin of Lake Erie (Holland 1993; Stapanian et al. 2009) and the clearer water has resulted in increased macrophyte growth (e.g., Schloesser and Manny 2007). Many areas of southern and western shorelines of the western basin of Lake Erie out to depths of a few meters support submerged attached and rooted aquatic vegetation. We hypothesize that vegetation corridors may function as avenues of expansion for tubenose gobies throughout western Lake Erie.

Tubenose gobies may also be moving seasonally in the Great Lakes in response to changing habitat conditions. Erös et al. (2005), using a PCA as we did, reported seasonal changes in habitat associations of monkey goby *Neogobius fluviatilis* and bighead goby *Neogobius kessleri* (now classified as *Ponticola kessleri* per Neilson and Stepien 2009) in the Danube River. They were unable to examine habitat associations and changes for tubenose goby owing to insufficient sample size. Trawl samples collected in June 2008 and 2009, early in the macrophyte growing season, produced no tubenose gobies at any sites (minimum depth 3 m). Trawl samples taken in October 2009 also produced no tubenose gobies. Autumn sampling in 2009 was 1 week later, and water temperatures were on average 1.5 to 2°C lower than in 2008. Similarly, tubenose gobies were captured at the northeastern tip of South Bass Island in October 2007, when macrophytes were present, but not in November 2007, when macrophytes were absent and water was cooler. Seasonal movements may be in response to presence of macrophytes and also may be linked to temperature. Additional research is needed to confirm seasonal migrations of tubenose gobies and environmental correlates of the migration.

Research to date suggests tubenose gobies may compete with several native Great Lakes species for feeding and reproduction sites. French and Jude (2001) reported substantial overlap between diets of rainbow darters *Etheostoma caeruleum* and tubenose gobies in June and December in the St. Clair River. Tubenose gobies and rainbow darters both preyed most frequently on dipterans in June and amphipods in December, but on both sampling dates those food items were available in abundance. Tubenose goby diet also overlapped with diets of northern madtom *Noturus stigmosus*, but the potential for competition may be low owing to different modes of foraging (French and Jude 2001). Tubenose gobies also have been reported to consume eggs and larvae of round gobies (French and Jude 2001). French and Jude did not report the presence of eggs of other species in tubenose goby diets and no eggs were sampled in the diet of freshwater tubenose gobies in this study.

Tubenose goby association with rocky substrates (Erös et al. 2005; French and Jude 2001; Jude and DeBoe 1996) and vegetation creates the potential for competition for space with rainbow darters. Jude et al. (1995) and Jude and DeBoe (1996) reported that tubenose gobies used small crevices in rocky areas to avoid predation, and both tubenose gobies and rainbow darters preferred shallower habitats (Gray et al. 1997; Greenberg 1991). Thus, habitat overlap for these two species is possible in nearshore areas of Lake Erie near river outflows where rainbow darters occur (e.g., in several tributaries to Lake Erie).

There also is potential for competition between tubenose gobies and johnny darters *Etheostoma nigrum* for spawning sites. Both species spawn on the underside of fixed objects such as rocks (Balon 1975; Jude et al. 1995). Tubenose gobies are similar in total length to johnny darters, but johnny darters are more slender and smaller in overall body size, which may provide a competitive advantage to tubenose gobies. Johnny darters were more abundant around the Bass Islands in the past (Trautman 1957), but were absent from our seine and trawl samples. They are still present in coastal wetlands and tributary streams.

Competition with logperch *Percina caprodes*, the most common darter species in Lake Erie, is less likely. Logperch bury their eggs in gravel, eliminating the potential for overlap in use of spawning sites. Both forage primarily on benthos, but French and Jude (2001) reported logperch consumed mostly

trichopterans and ephemeropterans whereas tubenose gobies consumed primarily dipterans in the only samples in which both species were captured in the St. Clair River. These differences suggest lower risk for competition between logperch and tubenose gobies.

In their native habitats, tubenose gobies are thought to inhabit a wide range of habitats including wetlands (Pinchuk et al. 2004) and rivers. However, the original tubenose goby species *Proterorhinus marmoratus* (now restricted to marine waters of the Black Sea proper, following phylogenetic assessment) was found to comprise several species, including the freshwater tubenose goby *P. semilunaris* that invaded the Great Lakes (Stepien and Tumeo 2006; Neilson and Stepien 2009); thus their habitats may be more specific than those reported in the literature. Expansion of the freshwater tubenose goby into and throughout western Lake Erie may include eventual colonization of the natural and reconstructed wetlands and major tributaries. Like round gobies, tubenose gobies may eventually become part of the forage base for predators, such as benthic-foraging yellow perch *Perca flavescens*, white perch *Morone americana*, smallmouth bass *Micropterus dolomieu*, burbot *Lota lota*, white bass *Morone chrysops* and walleye *Sander vitreus*, which all consume round gobies (Bunnell et al. 2005; Kocovsky et al. 2009). Presently there is no documented consumption of tubenose gobies by predators in Lake Erie.

Tubenose gobies are rare and even endangered in some native habitats (Economidis 1995) but they are established and now expanding in the Laurentian Great Lakes. The establishment of self-sustaining populations of freshwater tubenose gobies around the Bass Islands and their expansion into open waters of western Lake Erie suggest that new mechanisms of dispersal are responsible for the most recent expansion. Larval and juvenile drift at night coupled with currents created by the large volume of water entering Lake Erie from the Detroit River, where tubenose gobies have been established for many years, is a mechanism for dispersal of tubenose gobies throughout areas of western Lake Erie with suitable habitat. Vegetation corridors that connect Lake Erie's shorelines, nearshore wetlands, and tributaries, in addition to the currents created by the Detroit and Maumee Rivers, provide pathways for

dispersal throughout the remainder of Lake Erie and potentially into tributaries. Demonstrated overlap in habitat use, diets, and spawning sites between tubenose gobies and johnny and rainbow darters in particular, further suggest the potential for displacement of these native species. Other species with similar needs may also be affected.

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