J. Great Lakes Res. 34:450–460
Internat. Assoc. Great Lakes Res., 2008

Fish Assemblages and Environmental Variables Associated with Gobiids in Nearshore Areas of the Lower Great Lakes

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ABSTRACT. *We investigated which fish species and environmental variables were associated with the invasive round goby (Neogobius melanostomus) and tubenose goby (Proterorhinus marmoratus) in nearshore Canadian waters of the Huron-Erie corridor of the lower Great Lakes. We measured a suite of environmental variables and used triplicate beach seine samples to collect fishes in summer 2006. Thirty sites were sampled in the day and a subset (n = 14) at night. Of 1,955 individuals caught in daytime samples, round goby (21.0 %), spottail shiner (17.3%) and emerald shiner (14.2%) were most abundant. Of 1,521 individuals collected at night, the most abundant species were round goby (42.3%) and emerald shiner (24.1%). Tubenose gobies represented 1% and 1.7% of all individuals caught in the day and night, respectively. Rarefaction analysis showed that overall species richness was greater in the day than night. Significantly more emerald shiner (P = 0.017), rock bass (P = 0.046) and round goby (P = 0.035) were caught at night than in the day; more logperch were caught in the day than at night (P = 0.042). Round gobies were positively associated with water temperatures up to 24°, but there was no relationship between round goby abundance and warmer temperatures. There were too few tubenose goby captured to determine their statistical association with environmental factors; however, tubenose gobies were found only where round gobies were collected. Round goby and tubenose goby were associated with yellow perch and rock bass. The benthic round goby was the most abundant species, whereas other abundant species were pelagic, schooling fishes that occupied a habitat distinct from round goby.*

INDEX WORDS: *Environmental variables, fish assemblages, round goby, tubenose goby.*

INTRODUCTION

In freshwater ecosystems, invasive species are a significant threat to biodiversity (Sala *et al.* 2000). Although the Laurentian Great Lakes is not a global hot spot for invasive species (Drake and Lodge 2004), the region has a large number of aquatic invasive species (at least 182 species at present; Ricciardi 2006). Two invasive gobiid species, the round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus marmoratus*), were originally reported in the St. Clair River in 1990 (Crossman *et al.* 1992, Jude *et al.* 1992). Of all non-indigenous species within the Great Lakes, the round goby represents the fastest spreading vertebrate. Five years after the round goby was first reported, it had spread to all five Great Lakes (Charlebois *et al.* 1997). Nighttime vertical migration of round goby larvae and ballast transport likely accounted for the rapid dispersal of the species (Hensler and Jude 2007). Round goby are very abundant with an estimated population size in western Lake Erie alone in 2002 of 9.9 billion (Johnson *et al.* 2005a).

In contrast, the smaller tubenose goby is found infrequently in the Great Lakes. Its North American distribution is localized, occurring mainly in the

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Huron-Erie Corridor (H-EC) from the St. Clair River, Lake St. Clair, and the Detroit River to locations along the north shore of the western basin of Lake Erie (Leslie *et al.* 2002). Tubenose gobies also occur in shoreline areas of South Bass (2001, 2007), Middle Bass (2007), and North Bass (2007) islands in the western basin of Lake Erie (J. Tallman personal communication). In April 2001, a tubenose goby was caught in a trawl net by U.S. Geological Survey biologists in the Duluth Superior Harbor, western Lake Superior (Blust 2003). Since then, tubenose gobies and round gobies are commonly reported in regular monitoring programs in the Duluth-Superior Estuary Harbor region of western Lake Superior (Greg Peterson, U.S. EPA, Duluth and Dennis Pratt, Wisconsin DNR—Superior, personal communication). This jump dispersal by tubenose goby from the lower Great Lakes to Lake Superior can be explained by ship transport (Charlebois *et al.* 1997, Hensler and Jude 2007).

Despite differing distribution patterns of the round goby and tubenose goby in North American, both species are widespread in their native range. Specifically, the round goby is distributed widely throughout the Ponto-Caspian region and beyond, occurring in freshwater (lakes, reservoirs, and rivers), estuarine, and coastal habitats (Pinchuk *et al.* 2003). The tubenose goby also is widespread in its native Ponto-Caspian region and beyond, occurring in less saline estuaries, lakes, rivers, and wetlands (Pinchuk *et al.* 2004). Although the round goby has spread to the Gulf of Gdansk and Baltic Sea, the tubenose has not yet invaded that region (Pinchuk *et al.* 2004).

The success of the round goby is likely due to its broad diet (crustaceans, soft-bodied macroinvertebrates, dreissenids), aggressiveness, high fecundity, repetitive annual spawns, and male parental care (Corkum *et al.* 2004). Although tubenose goby may eat mussels in their native range (Pinchuk *et al.* 2004), their diet in the Great Lakes is mainly amphipods, crustaceans, and insects (French and Jude 2001). Drake (2007) showed that parental care (not fecundity or brain size, a correlate of cognitive ability) was associated with establishment success in introduced species. It is unclear why tubenose gobies have played a seemingly minor role as an invasive species. Because males of both round goby (MacInnis and Corkum 2000) and tubenose goby (Ahnelt *et al.* 1998) guard embryos, parental care does not explain the differential success of these species. In other gobiids, habitat use and preference (macrophytes) account for the differentiation in success (Humphries and Potter 1993).

In this study, we determined which fishes were associated with round goby and tubenose goby and which environmental variables accounted for their distribution in the H-EC, the area of their original colonization in the Great Lakes. We also wondered if these species were day or night active (as determined by numbers captured in beach seines) and if this activity was a function of their body size. We expected small (vs. large) gobies to be more active at night because predation risk is perceived to be greater during the day (cf. Clark and Levy 1988).

METHODS

Sampling and Study Sites

This field study was designed to examine fish assemblages and environmental factors associated with round goby and tubenose goby in the H-EC. Ten sites were sampled in each of the following locations: Lake St. Clair (including a part of the St. Clair River), Detroit River, and Lake Erie (Fig. 1).

In summer (June–August) 2006, we collected fishes by beach seining (triplicate samples) along the Canadian H-EC shoreline. The seine net was 9.1 m in length and 1.8 m deep (mesh size: 6.4 mm) with a bag 1.8 m long × 1.8 m deep (mesh size: 3.2 mm). The seine was deployed perpendicular to shore for its entire length and then swept back in an arc to the shore. We selected sites that could be accessed safely. Because sampling sites were separated by at least one tributary, we assumed that the sites represented independent samples. Daytime sites (n = 30) were sampled between 0830 and 2100 hours. Nighttime sites (n = 14) were selected from a subset of corresponding daytime sites (Fig. 1) and were sampled within 48 h of the date of the new moon between 2105 and 0545 hours**.** Of the 14 sites, four were sampled along Lake Erie, four along Detroit River, four along Lake St. Clair, and two along St. Clair River. Nighttime samples were taken during the new moon because moonlight is known to affect fish dispersal (Wickham 1973).

Twelve environmental variables measured at each site were aquatic macrophytes (present/absent; simple/complex), depth and maximum distance from shore where fishes were seined, elevation (GPS device, Magellan®), floodplain vegetation, riparian vegetation, shoreline type, slope, substrate, turbidity, water temperature, and water body. If present, aquatic vegetation was scored as simple or complex (Lapointe *et al.* 2007) because the morphological

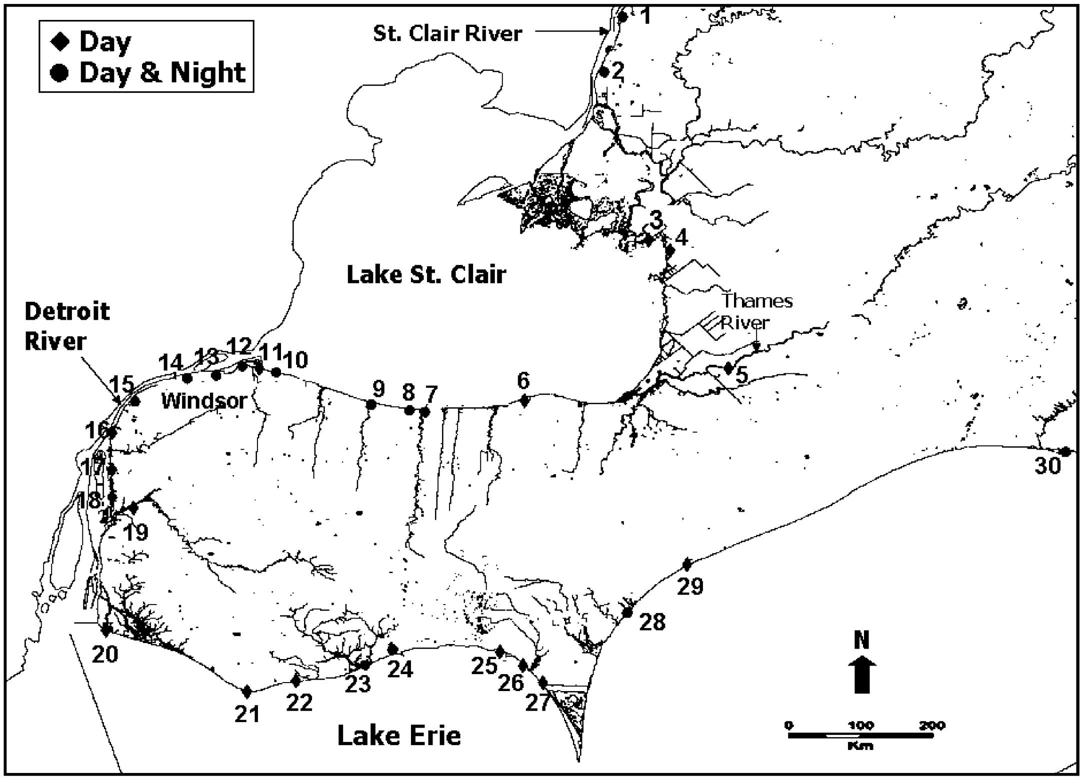

FIG. 1. Location of sampling sites in the Huron-Erie corridor, summer 2006. Diamond symbols represent the 30 daytime sampling sites; circles represent sites sampled in the day and night.

structure of aquatic macrophytes affects the quality of habitat for fishes (Petry *et al.* 2003). Simple vegetation described plants with long grass-like leaves such as eel grass (*Vallisneria americana*). Complex vegetation included plants with multiple branching leaves (e.g., *Ceratophyllum demersum*). Values were recorded as present/absent for simple, complex, or both vegetation types. Shorelines were classified as either beaches or tributaries. Floodplain vegetation (i.e., grass, shrubs, or trees) was recorded as a description of the land use in the area where fishes were seined. Riparian vegetation was estimated as a percentage of vegetation adjacent to the water. Slope of the land adjacent to the water was determined using a pocket transit (Brunton ®). Substrate was estimated visually as fine (coarse sand, 0–2 mm, or finer) or coarse (small gravel ≥ 2 mm) (Lapointe *et al.* 2007). Turbidity (obtained using a turbidity tube) values represented the amount of sediment suspended in water.

All fish species caught were identified using appropriate keys (Scott and Crossman 1973, Becker 1983, Page and Burr 1991, Hubbs and Lagler 2004). Fish species, except for round goby and tubenose goby, were released on site. However, if a fish could not be identified, it was returned live to the laboratory for identification. The total length of all gobies caught was measured.

Data Analyses

We initially tallied all species collected at the 30 sites. We defined dominant taxa as those that represented at least 1% of the total number of daytime individuals caught (n = 1955) and were present at 3 or more of the 30 sites. Species richness estimates depend on the number of individuals in a sample (Gotelli and Colwell 2001). We compared species richness between the 14 day and night matched sampling sites, using a rarefaction-sampling algorithm with repeated re-sampling of smaller numbers of individuals from the larger dataset (*Estimate S* software, Colwell 2005). A repeated measures (rm) ANOVA was used to determine differences in species abundance between the 14 day and night matched collections for the dominant fishes. A twoway ANOVA was used to determine the influence of site location and/or photoperiod on total length (TL) of round and tubenose gobies. Stepwise multiple regression analysis was used to determine which environmental factor(s) explained the greatest variability in the round goby and tubenose goby abundance from the 30 sites. To determine species associations, we used a principal component analysis (PCA) based on a correlation matrix performed on the $\log_{10}$ abundance of the dominant 15 fish taxa collected at the 30 (daytime) sites. All statistical analyses were performed using Statistica version 7, using a critical alpha value of 0.05 to test hypotheses.

RESULTS

We captured 1,955 fishes (12 families, 31 species) in 90 (30 sites × 3 hauls/site) daytime seine hauls (Table 1). The common and scientific names (according to Nelson *et al.* 2004) of the species captured are provided in Table 1. Round goby, spottail shiner, emerald shiner, white perch, and brook silverside were the most abundant species collected during the day (Table 1). The 42 (14 sites × 3 hauls/site) nighttime seine hauls yielded 1,521 fishes (10 families and 24 species). Overall, round gobies were present at 22 of the 30 sites sampled and tubenose gobies were present at 9 of all sites

TABLE 1. Species (scientific and common names according to Nelson* et al. *(2004)) captured by seining in the study area, 2006, and codes used to represent them. Species code is derived from the first two letters of the scientific genus and species names, respectively. Abundance is total abundance for each species caught during daytime sampling (n = 30 sites). Total abundance was 1955.

Scientific Name	Common Name	Code	Abundance
Alosa pseudoharengus	Alewife	ALPS	97
Ameiurus natalis	yellow bullhead	AMNA	3
Ameiurus nebulosus	Brown bullhead	AMNE	11
Ambloplites rupestris	rock bass	AMRU	22
Aplodinotus grunniens	freshwater drum	APGR	4
Carassius auratus	Goldfish	CAAU	5
Catostomus commersonii	white sucker	CACO	12
Cyprinus carpio	common carp	CYCA	2
Dorosoma cepedianum	gizzard shad	DOCE	68
Esox lucius	northern pike	ESLU	1
Fundulus diaphanus	banded killifish	FUDI	4
Hypentelium nigricans	northern hog sucker	HYNI	4
Ictalurus punctatus	channel catfish	ICPU	9
Labidesthes sicculus	brook silverside	LASI	171
Lepomis gibbosus	Pumpkinseed	LEGI	40
Lepomis macrochirus	Bluegill	LEMA	85
Lepomis megalotis	longear sunfish	LEME	3
Lepisosteus osseus	longnose gar	LEOS	7
Micropterus dolomieu	smallmouth bass	MIDO	53
Micropterus salmoides	largemouth bass	MISA	9
Morone americana	white perch	MOAM	193
Morone chrysops	white bass	MOCH	21
Neogobius melanostomus	round goby	NEME	411
Nocomis biguttatus	hornyhead chub	NOBI	13
Notropis atherinoides	emerald shiner	NOAT	278
Notropis hudsonius	spottail shiner	NOHU	338
Perca flavescens	yellow perch	PEFL	32
Percina caprodes	Logperch	PECA	30
Pimephales notatus	bluntnose minnow	PINO	7
Pomoxis nigromaculatus	black crappie	PONI	1
Proterorhinus marmoratus	tubenose goby	PRMA	17
Others			6

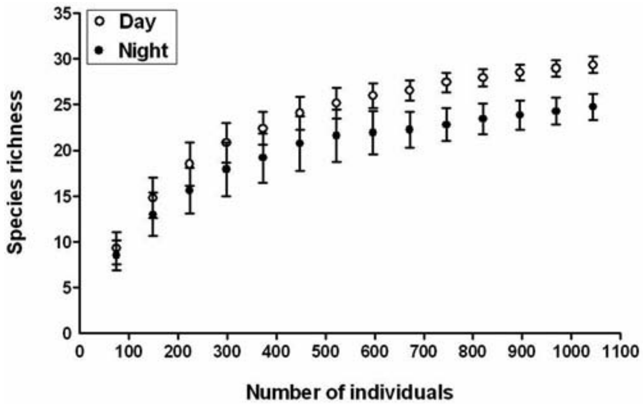

FIG. 2. Day (open circles) and night (closed circles) individual-based species rarefaction curves (± 95% CI) from seining data.

sampled. Round gobies were found throughout the Huron-Erie Corridor, whereas tubenose gobies occurred in the St. Clair River, Lake St. Clair, and Detroit River. Tubenose gobies were found only where round gobies were collected.

Rarefaction analysis showed that overall species richness was greater in the day than night once 400 or more individuals were sampled (Fig. 2). Results of the rmANOVA indicated there were significant differences between abundance of fishes sampled in the day and night at matched sites (Wilks' value = 0.215, $F_{(12,15)} = 2.913$, $p = 0.034$) (Table 2). Significantly more emerald shiners ($p = 0.017$), rock bass ($p = 0.046$), and round gobies ($p = 0.035$) were caught at night than in the day; and, significantly more logperch were captured in the day than at night ($p = 0.042$) (Table 2). Mean (standard error) abundance of round goby at night (46 ± 9.00) was twice that of day (23 ± 5.17) collections at matched sites. Although we caught more tubenose gobies in night samples (1.7 ± 0.82; n = 24) than in day samples (1 ± 0.49, n = 17), the mean abundance was not significantly different.

The range in body size (total length) for tubenose gobies (28 to 60 mm) was less than the range in body size for round gobies (15 to 120 mm). There was a significant size difference in round gobies among waterbodies ($F_{2,\ 1123} = 129.85$, $p < 0.0001$), between day and night ($F_{1,\ 1123} = 20.14$, $p < 0.0001$) and the interaction between the two variables ($F_{2,\ 1123} = 14.47$, $p < 0.0001$). The largest size difference between day (mean ± SE: 57.2 mm ± 1.15) and night (46.6 mm ± 0.80) for round gobies was in the Detroit River. Round gobies collected in Lake St. Clair/St. Clair River (day: 38.4 mm ± 1.29; night: 36.9 mm ± 1.10) were smaller than those collected from western Lake Erie (day: 53.2 mm ± 1.49; night: 54.7 mm ± 1.13). Larger tubenose gobies were caught at night (48.9 mm ± 1.90) than day (41.2 mm ± 3.31) in the Detroit River ($F_{1,37} = 5.11$, $p < 0.03$).

Results of the multiple regression analysis

TABLE 2. Comparison of day and night abundance and frequency for dominant fishes at 14 sites. The overall rmANOVA on abundance of fishes sampled in the day and again at night was significant (P = 0.034.) Probability (P) values are provided for species that exhibited significant differences in abundance between day and night samples. NS, not significant.

	Mean number (SE)			% Sites	
Species	Day	Night	P	Day	Night
alewife	4.8 (2.89)	0.5 (0.50)	NS	36	7
bluegill	1.1 (0.55)	1.86 (1.44)	NS	29	21
brook silverside	7.6 (2.95)	9.8 (3.51)	NS	70	64
channel catfish	0.5 (0.37)	2.3 (1.51)	NS	14	21
emerald shiner	11.4 (3.16)	26.21 (5.39)	0.017	86	100
gizzard shad	1.8 (1.30)	1.7 (1.22)	NS	14	29
logperch	1.4 (0.56)	0.14 (0.10)	0.042	43	14
rock bass	0.9 (0.41)	3.0 (1.09)	0.046	36	79
round goby	23.0 (5.17)	46.0 (9.00)	0.035	93	100
smallmouth bass	1.2 (0.61)	0.71 (0.35)	NS	29	29
spottail shiner	9.8 (4.18)	9.29 (3.34)	NS	64	64
tubenose goby	1.0 (0.49)	1.7 (0.82)	NS	29	36
white perch	3.3 (1.54)	1.9 (1.44)	NS	36	43
yellow perch	1.8 (0.93)	0.43 (0.23)	NS	29	29

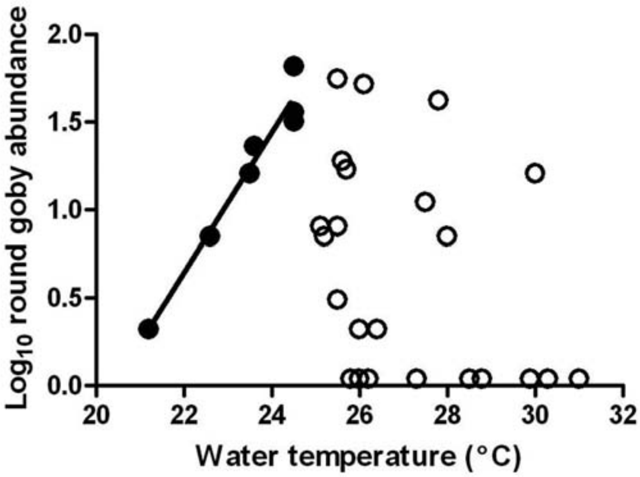

FIG. 3. The relationship between water temperature and the log10 round goby abundance. Round goby abundance was significantly associated with water temperature up to 24°C (indicated by closed circles and the straight line); open circles represent round goby abundance at higher temperatures.

showed that three environmental factors accounted for the overall significance of round goby abundance ($R^2 = 0.67$, df= 8, 20, $p = 0.022$). Water depth (35 to 115 cm) was positively correlated ($t_{(20)} = 3.67$, $p = 0.001$) with round goby abundance; whereas, water temperature, 21 to 31°C ($t_{(20)} = -3.02$, $p = 0.008$) and turbidity, 5 to 115 cm ($t_{(20)} = -2.87$, $p = 0.01$) were negatively correlated with abundance. The relationship between round goby and water temperature was complex. Round goby abundance was positively correlated with water temperature up to 24°C, but after this threshold, there was no relationship between round goby abundance and warmer temperatures (Fig. 3). Interestingly, spawning activity appears to have a 25°C threshold (Corkum, personal observations). Depth and turbidity affected round goby abundance when interacting with other factors, but not when analyzed alone. The overall multiple regression analysis for tubenose goby was not significant.

Results of the PCA showed that the first three components explained only 46.5% of the variability in the data (Table 3). There was no apparent arch effect in the data, indicating that non-linearity was not a problem. In the plot of the first two principal components, round goby, tubenose goby, and yellow perch occupied the origin; however, emerald shiner, spottail shiner, logperch, and brook silverside were distinct from smallmouth bass /rock bass, pumpkinseed/bluegill, and the other fishes (Fig. 4). Both goby species were highly correlated with PC3. The plot of the first and third components best illustrate the association between the gobiids and other fishes. Both rock bass and yellow perch were associated with gobiids to form one grouping of fishes (Fig. 4). Bluegill, pumpkinseed, and smallmouth bass grouped together, and all remaining fishes formed a third association (Fig. 4).

TABLE 3. PCA results based on the abundance of the 15 most frequently encountered fishes collected from 30 sites sampled in the daytime along the Huron-Erie corridor in nearshore Canadian waters. The factor scores, eigenvalues and cumulative percentage variance are presented for the first three components. Fishes are listed alphabetically by species code and common name (see Table 1).

CODE	Common name	PC1	PC2	PC3
ALPS	alewife	0.476	–0.538	0.076
AMRU	rock bass	–0.253	0.283	0.495
DOCE	gizzard shad	0.712	–0.137	–0.064
LASI	brook silverside	0.266	0.263	–0.020
LEGI	pumpkinseed	–0.439	–0.203	–0.295
LEMA	bluegill	–0.444	–0.510	0.050
MIDO	smallmouth bass	–0.528	0.423	–0.129
MOAM	white perch	0.5583	–0.304	0.262
MOCH	white bass	0.755	–0.101	–0.176
NEME	round goby	–0.036	0.009	0.813
NOAT	emerald shiner	0.442	0.697	–0.132
NOHU	spottail shiner	0.084	0.761	0.010
PECA	logperch	0.382	0.373	0.196
PEFL	yellow perch	–0.069	–0.045	0.465
PRMA	tubenose goby	–0.017	0.006	0.726
Eigenvalue		2.802	2.246	1.922
Cumulative percentage variance		18.68	33.65	46.46

DISCUSSION

The bottom-dwelling round goby was the most abundant fish species along the H-EC. Other abundant species in our study (brook silverside, emerald shiner, spottail shiner, and white perch) were pelagic, schooling fishes (Becker 1983) that occupy a habitat distinct from round goby. Lapointe *et al.* (2007) reported that emerald shiner, spottail shiner, and round goby were the first, third, and seventh most abundant fishes captured using boat seines in offshore, shallow (< 2.5 m) Canadian waters of Detroit River in 2004 (May, July, and September). Spawning emerald shiner dominated the May col-

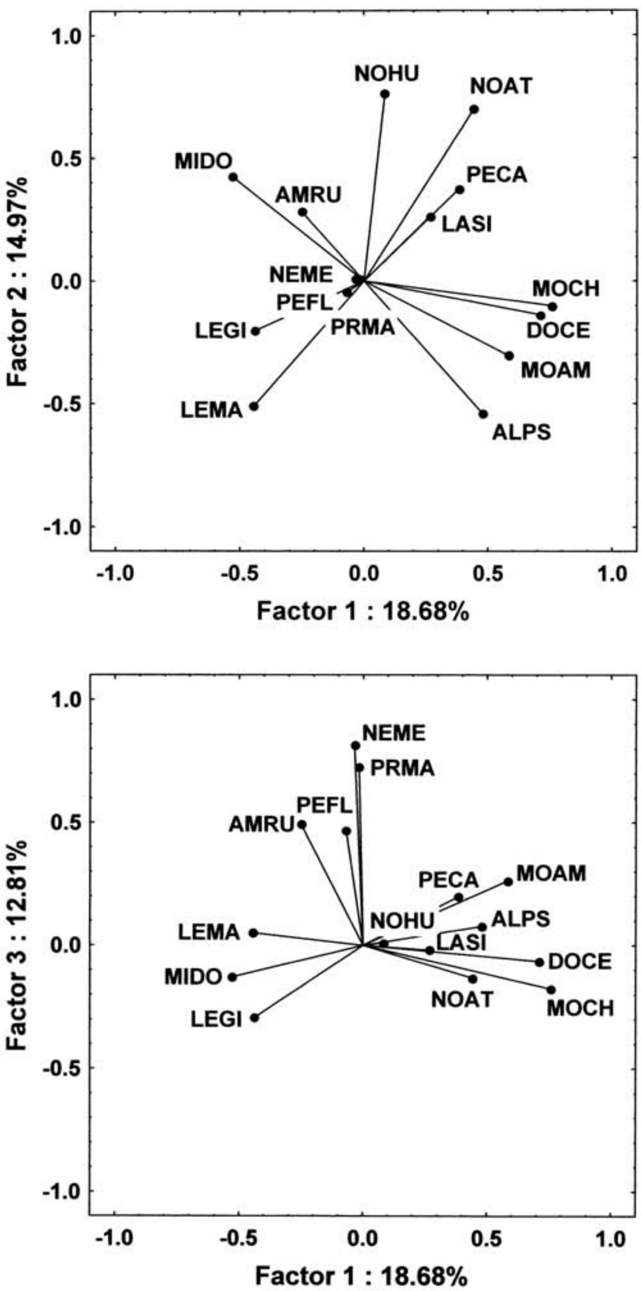

FIG. 4. Plot of the first and second principal component (upper panel) and the first and third principal component (lower panel) analysis based on the abundance of the dominant 15 fishes collected at 30 sites in the day. Refer to Table 1 for species codes.

lection, representing 78% of the catch (Lapointe *et al.* 2007). Thomas and Haas (2004) reported that, although round goby and tubenose goby were widespread throughout Lake St. Clair, round goby were far more abundant than tubenose goby. Round goby was the third most abundant species caught (after mimic shiner and spottail shiner) in nearshore trawls (1996 to 2001) of Lake St. Clair, representing 5.5% of the catch (n = 2,701); tubenose goby represented 0.3% of the catch (n = 165) (Thomas and Haas 2004).

Overall, fish species richness was higher in daytime than nighttime samples. However, these diel differences were not strong, supporting the findings of Diers *et al.* (2001). Of the dominant species, significantly more emerald shiner, rock bass, and round goby were collected at night than day; whereas, more logperch were collected in the day than night. Round goby represented double the proportion of fishes caught at night compared to daytime collections. This nighttime activity may be related to their foraging habits, e.g., avoidance of visual predators (Eros *et al.* 2005). In contrast, higher densities of large (> 50 mm) round goby on rocks have been reported in the day than night in the Detroit River, Lake St. Clair, and the St. Clair River using SCUBA surveys (Ray and Corkum 2001), which was corroborated by our Detroit River findings, suggesting that round gobies were able to avoid visual predators in this water body due to size differences.

Although round gobies captured in the day were significantly larger than those captured at night in the Detroit River, day-night size differences were not evident in the other locations we examined. Small round gobies seem to disperse to sandy areas where there is an abundance of soft-bodied prey and conspecific adults are fewer (Jude *et al.* 1995, Ray and Corkum 2001). Fine substrates characterized most of our seining sites where younger (i.e., smaller) gobies are found. Larger round gobies may avoid capture by gape limited, diurnal piscivores. Differences in size of tubenose goby between night and day depended on sample location.

In our study, round goby were most prevalent in deeper, clearer waters. Although there was no relationship between round goby abundance and elevated water temperatures (> 25°C), we found a direct relationship between round goby abundance and water temperature up to 24°C. Lee and Johnson (2005) showed that maximum consumption (i.e., an estimate of the amount of food consumed under optimal conditions) for round gobies showed a strong relationship with temperature. Interestingly, they showed that maximum consumption increased with temperature up to 26°C, after which consumption rates declined abruptly. Moreover, 25°C has been documented as the upper limited for spawning (Bilko 1968).

We collected too few tubenose goby to determine their statistical association with environmental factors. Leslie *et al.* (2002) collected tubenose goby in water with no or slow flow on clay or alluvium substrates, where turbidity varied and where rooted vegetation was sparse, patchy or abundant. Jude *et al.* (1995) reported that tubenose lay their eggs in eel grass and so may be closely associated with the plant, yet Lapointe (2005), who used a boat seine, showed that tubenose goby were only associated with macrophytes in autumn. In a large-scale study of nearshore waters in the Great Lakes, where fyke nets were used to catch fishes, tubenose gobies were never caught (V. Brady, NRRI, personal communication).

The prevalence of the bottom-dwelling round goby in our study may explain the limited number of other benthivores captured. Only one mottled sculpin (*Cottus bairdii*) and a few logperch, but no other darters, were collected at our study sites, supporting the notion of Jude *et al.* (1995) that the invasive round goby will lead to the decline of native benthic fishes. However, without data prior to the invasion of gobiids, the absence of sculpins or darters cannot be attributed to the presence of gobiids (especially, the round goby). In a study of changes in nearshore fish communities at 34 sites in Lake Erie before and after goby invasion, Reid and Mandrak (2008) noted the dramatic decline in benthic fishes including logperch and trout-perch (*Percopsis omiscomaycus*), and complete loss of channel darter (*Percina copelandi*), johnny darter (*Etheostoma nigrum*), mottled sculpin, and slimy sculpin (*Cottus cognatus*). They attributed these declines and losses to a variety of factors including round goby invasion. The round goby has been shown to out-compete native fishes, such as logperch, for space (Balshine *et al.* 2005) and mottled sculpin for shelter, food, and nest sites (Dubs and Corkum 1996, Janssen and Jude 2001).

The H-EC study area in the lower Great Lakes is known for its piscivores (muskellunge (*Esox masquinongy*), smallmouth bass, walleye (*Sander vitreus*), and yellow perch) and diverse forage fish community (Thomas and Haas 2004). The results of our study revealed an association among round goby, tubenose goby, yellow perch, and rock bass. Although round gobies are the dominant benthivore in western Lake Erie, rock bass, yellow perch, and smallmouth bass commonly co-occur on shipwrecks and other rubble areas (Wickett and Corkum 1998, Thomas and Haas 2004). Rock bass, smallmouth bass, yellow perch, and other piscivores are known to feed on round goby (Jude *et al.* 1995, Thomas and Haas 2004, Johnson *et al.* 2005b, Truemper and Lauer 2005). Thomas and Haas (2004) reported that, in Lake St. Clair, round gobies were the most frequently encountered fish in yellow perch stomachs and the second most frequent food item in walleye. Moreover, the fish diet of yellow perch shifted from brook stickleback, johnny darter, and slimy sculpin in 1993 to round gobies and age-0 bluegill and pumpkinseed in 2000 (Thomas and Haas 2004).

Little is known about tubenose goby in the Great Lakes because of their low abundance. Within the Great Lakes, tubenose goby have remained mostly within the H-EC but have been recorded in western Lake Erie (Stepien and Tumeo 2006, J. Tallman personal communication) and the Duluth-Superior Estuary Harbor region of western Lake Superior (Blust 2003). Although we captured tubenose goby at sites along the St. Clair River, Lake St. Clair, and the Detroit River, we did not collect any specimens from western Lake Erie sites. In Lapointe's (2005) fish-habitat study on the Detroit River, only 22 tubenose goby were captured. This rare species was present in 16 of 180 boat seines and only one tubenose goby was captured at 165 electrofishing sites (Lapointe 2005). Elsewhere, Eros *et al.* (2005) reported that tubenose goby exhibited low densities and a patchy distribution in the Danube River.

In summary, nearshore fish assemblages in the H-EC are now dominated by a single benthivore, the invasive round goby, and schooling pelagic forage fishes. Although we were unable to determine which environmental factors influenced the abundance of tubenose goby (in part because of the few specimens collected), tubenose goby were always present at sites where round goby were found. The feeding habits of small round gobies and tubenose gobies on plankton and macroinvertebrates (French and Jude 2001) may represent a loss of available prey to other forage fishes, both benthic and pelagic.

It is a puzzle to understand why these two benthic invaders that arrived in the Great Lakes about the same time exhibit differential success, especially in their ability to spread. Clearly, the larger round goby is more widespread and abundant than the smaller, rarer tubenose goby. Our study was not designed to determine why one invader has been successful, whereas another "somewhat related" (divergence between the species occurred about

5.2±1.0 million years ago; Dillon and Stepien 2001) species has not. However, we can provide some speculations. Round gobies are found as far as 34 km offshore in waters 73 m deep (Schaeffer *et al.* 2005), whereas tubenose gobies dwell in shallow (4 m or less) nearshore waters (Pinchuk *et al.* 2004). Given reported shifts to oligotrophy in some nearshore waters (Madenjian *et al.* 2002) and the more restricted diet (i.e., one without dreissenids) of tubenose goby, this species is likely more sensitive to shifts in prey than round goby. Also, the reported link between tubenose gobies and wetlands (Pinchuk *et al.* 2004) suggests that a decline in wetland habitat may explain the low occurrence of the tubenose goby. Whereas the round goby exhibits aggressive behavior with respect to other species (Dubs and Corkum 1996), aggressive behavior has not been observed in the tubenose goby. Johnson *et al.* (2005b) showed that round gobies are a major vector in the transfer of energy through the food web in Lake Erie. Tubenose gobies have not yet exhibited any ecosystem effects of which we are aware. Further field and lab observations, as well as manipulative experiments, should help to explain the differential success of these species and to understand their ecological interactions and ecosystem effects.

ACKNOWLEDGMENTS

Funding for this research was provided by the Department of Fisheries and Oceans Canada. We thank John Kosciuw for field assistance. Greg Petersen (U.S. EPA Duluth) and Dennis Pratt (Wisconsin DNR) kindly provided unpublished data on the round goby/tubenose goby monitoring program in the Duluth-Superior region of western Lake Superior. Val Brady (NRRI, Duluth) and John Tallman also provided information. We thank Misun Kang, Nicolas W.R. Lapointe, Geoffrey B. Steinhart, and two anonymous reviewers for their constructive comments on an earlier draft of the paper.

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Submitted: 6 January 2008
Accepted: 30 April 2008
Editorial handling: Geoffrey Steinhart