**Diel Vertical Migration of Round Goby Larvae in the Great Lakes**

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**ABSTRACT.** One hypothesis for the transcontinental and intra-Great Lakes basin transfer of round gobies (Neogobius melanostomus) has been that round gobies were pumped into the ballast water of ships. During June 2005 in Lake Erie, we obtained evidence of a vertical migration of round goby larvae, when we collected 167 round goby larvae in surface ichthyoplankton net tows at night and zero during day. These results complemented similar findings from the Muskegon River estuary of Lake Michigan during 2003 and 2004, documenting diel vertical migration for the first time in larval round gobies. We suggest vertical migration behavior may have allowed larval round gobies to be transported to and within the Great Lakes via ballast water and dispersed in the Great Lakes via advection of 6.5–8.5-mm long larvae at the surface. Based on our results, if ballast water was only taken on near the surface during daylight hours from May through September when larval round gobies were present, it would have mitigated the spread of round gobies throughout the Great Lakes.

**INDEX WORDS:** Round goby, ballast water, larval fish.

**INTRODUCTION**

The round goby (Neogobius melanostomus), a nonindigenous fish species, was transported to the St. Clair River sometime before 1990 via the ballast water of foreign freighters (Jude et al. 1992). Subsequently, round gobies were transported, presumably by Great Lakes freighters, to major Great Lakes ports, which then became donor regions fostering the spread of this exotic species, during the 1990s and early 2000s. The mechanism for round and tubenose (Proterorhinus marmoratus) goby transport aboard freighters has proven elusive to confirm. Freighters take in ballast water in ports from 6 to 9 m below the surface (H. MacIassac, University of Windsor, Windsor, Ontario, Canada, personal communication) and also from the surface (R. Harkens, Lake Carriers’ Association, Cleveland, Ohio, U. S. A. personal communication) using pumps (Locke et al. 1993). These ships run 24 h per day, and timing of ballast water uptake is random (some occur during day, some at night), but taking on ballast water too close to the bottom is avoided to keep debris from becoming entrained in a ship ballast water tank (R. Harkens, Lake Carriers’ Association, Cleveland, Ohio, U. S. A. personal communication). Round gobies are a benthic species without swim bladders and have benthic larvae (Miller 1984), which led Jude et al. (1995) and Jude (2001) to hypothesize that round gobies may have been transported by: 1) laying eggs in crevices of the hull of a ship, 2) being pumped into the ballast water of the ship, or 3) somehow becoming sequestered in hoses or holes on a ship (see Gollasch et al. 2002, Wonham et al. 2000) and were subsequently transported to a new port.

Larval round gobies have not been known to undergo diel vertical migrations, but at least one other species in the family, the naked goby (Gobiosoma bosc), is known to exhibit such behavior (Schultz et al. 2003). Naked goby larvae in the Hudson River estuary come near shore and to the surface at night during spring, particularly on neap tides, and use currents to carry them upstream. Additionally, they remain in the water column as they grow, but larval naked gobies tend to be found at deeper depths as they grow larger.

Invasive organisms that have pelagic life stages, like the pelagic veliger stage of zebra (Dreissena polymorpha) and quagga (D. bugensis) mussels (Hebert et al. 1989, Garton and Haag 1992), and the
zoo plankter Cercopagis pengoi (Charlebois et al. 2001), have an enhanced ability to colonize other water bodies. Pelagic veligers were probably responsible for the rapid dispersal of dreissenid mussels throughout the Great Lakes through natural movement of water currents (Beletsky et al. 1999), uptake in the ballast water of intra-lake freighters (Mills et al. 1993), and bait-bucket transfers (Jude 2001). Ballast water has been identified as a vector for transport of various fishes, including several Gobiidae species (Brittan et al. 1963, Biro 1972, Hoese 1973, Williams et al. 1988, Gollasch et al. 2002). Non-indigenous species have been transported both to the Great Lakes from foreign ports as well as within the Great Lakes from one area to another (Mills et al. 1993), including strongly demersal species such as round and tubenose gobies (Jude et al. 1992) and European flounder (Platichthys flesus) (Emery and Teleki 1978, Crossman 1984). Ricciardi and Rasmussen (1998) suggested that many more non-indigenous species from the Black and Caspian seas area are potential threats because of their biological characteristics and history of invasion in other water bodies, probably using ballast water as a vector of dispersal. Hence we require information on how those species are getting into and being transported throughout the Great Lakes to attempt to manage this problem of dispersal of exotic species.

The objective of this study was to document diel vertical migration of round goby larvae in the Great Lakes. After incidentally collecting larval round gobies in surface ichthyoplankton samples in and around the Muskegon River estuary of Lake Michigan, we conducted additional sampling in western Lake Erie to help determine if larval round gobies purposefully or incidentally migrate upward in the water column. Implications of our findings with regard to larval fish dispersal and ballast water transport of round gobies suggest that these fish do enter the water column and may be transported widely in freighters.

**METHODS**

Larval fishes were collected in surface (top 1 m of water) ichthyoplankton net tows at night from May to July 1999–2002 in the Muskegon Harbor channel leading to Lake Michigan (43° 13′ 40” N, 86° 20′ 23” W) and over the 3- and 6-m depth contours in Lake Michigan near Muskegon, MI (3 m 43° 13′ 00” N, 86° 20′ 08” W; 6 m 43° 12′ 58” N, 86° 20′ 15” W), as part of a yellow perch recruitment study. During 2003 and 2004, these same sites were sampled as were the mouths of the Muskegon River (north branch 43° 15′ 38” N, 86° 14′ 55” W; south branch 43° 14′ 58” N, 86° 14′ 39” W), four other sites in the lower Muskegon River below Croton Dam, and 21 other sites in Muskegon Lake (two others during 2003, 19 others during 2004). In Lake Michigan during 1999–2002, three replicate samples were collected in 10-min surface tows of a neuston net (1 m × 2 m; 500-, 1,000-, and 1,800-µm mesh—see Dettmers et al. 2005) and one 5-min surface sample was collected with a 0.75-m diameter, 363-µm-mesh net at 3- and 6-m depths. From 1999 to 2002, 104 tows were conducted with the neuston net, while 10 tows were conducted with the 0.75-m diameter, conical net. During 2003, all 79 ichthyoplankton samples taken in Muskegon Lake and nearshore Lake Michigan when larval round gobies may have been present (June and July) were collected during day. In 2004, 22 samples were collected in Muskegon Lake when larval round gobies may have been present (June), but all 2004 ichthyoplankton sampling at the surface occurred at night.

After we collected round gobies in surface tows during 2000 and knowing round goby larvae were benthic, we initiated a series of bottom sled tows to learn more about densities on the bottom at our Muskegon study site during 2001. This device was composed of an ichthyoplankton net housed in a sled apparatus (Madenjian and Jude 1985) towed along the bottom during the day at each of the 3- and 6-m depth contours in Lake Michigan only. Sled sampling was only performed during the day, because sampling for larval round gobies was not funded, and we devoted our efforts at night to sampling our funded yellow perch recruitment research. Eleven tows were performed with the benthic sled. In the channel between Muskegon Lake and Lake Michigan (9-m deep), one 5-min surface tow using the 0.75-m diameter, conical net was conducted at night in conjunction with larval fish sampling occurring in Lake Michigan during 1999–2002; 10 tows were completed at this site. All nets were equipped with flowmeters (Jude 1992). Surface sampling took place at night to reduce net avoidance.

Collection of larval round gobies in surface net tows led us to hypothesize that round goby larvae performed a diel vertical migration, and since we only had night data at the Muskegon site, we sampled in Lake Erie, where round gobies are much more abundant. An additional series of surface, 5-min, towed samples were completed during 2003
and 2005 in Lake Erie. During 2003 in Lake Erie, we sampled once at night on 28 July and once during the day on 30 July. Samples were collected for 5 min each with a 0.75-m diameter, 500-micron-mesh net in 6 m of water west of Gibraltar Island in the western basin of Lake Erie. No flow meter was available for this net. During 2005, the neuston net described above equipped with 500-micron mesh and a flow meter was deployed for 5 min during two day (18:00 Eastern Standard Time (EST), 09:30 EST) and two night (23:00 EST, 02:30 EST) periods on 27–28 June at two sites (3 m, 9 m) north of Peach Point off South Bass Island, Lake Erie (3 m, 41°39′675 N, 82°49′433″ W; 9 m, 41°39′667″ N, 82°49′669″ W). Two replicate samples were collected at each depth contour during each time period resulting in a total sample size of 16.

All samples were concentrated then preserved with ethanol in the field. Larval fish were sorted in the laboratory, total length measured to the nearest 0.5 mm, and identified using Auer (1982) and preserved larval round gobies hatched from eggs previously collected in the field. Larval round gobies were easily distinguished from larvae of native benthic fishes (e.g., sculpins), as their fused pelvic fins were obvious even on specimens still in the yolk-sac stage. Wave height was estimated visually for all samples (1999–2005), while surface water temperature was measured with a YSI model 51A, dissolved oxygen-temperature meter (alpha = 0.05) was conducted to test for significance of day/night density differences for Lake Erie samples collected in 2003 and 2005. Linear regressions were performed using surface densities of larval round gobies collected during June, July, and August 2000 to 2004 in the vicinity of the Muskegon River estuary against wave height, depth, and water temperature to identify relationships between physical factors and presence of round gobies.

RESULTS

No larval round gobies were collected during 1999, but we did collect them in low densities beginning in 2000; only three were found in the sled and they ranged from 9 to 19 mm total length (TL). Larval round gobies (n = 208) from 6.0 to 8.9 mm TL (Fig. 1) were collected in surface ichthyoplankton net tows in Lake Michigan, Lake Erie, and the Muskegon River near its mouth to Lake Michigan (Table 1). All were collected during June-August and most fish were 7–8 mm long (98%). No larval round gobies longer than 8.9 mm TL were collected at the surface. There were 16 collected in Lake Michigan, 9 in the Muskegon River, 9 in the channel between Muskegon Lake and Lake Michigan, and 167 from Lake Erie. In Lake Michigan, only one was caught during the day (in a sled tow), while 15 were caught at night (in surface tows). In Lake Erie, all 167 larval round gobies collected during 2005 were collected at night (mean night density = 45 larvae / 1,000 m$^3$) (Fig. 2), resulting in a significant diel difference ($\chi^2 = 167$, df = 1, $p < 0.0001$) based on a chi-square test for goodness of fit. During 2003 in Lake Erie, nine larval round gobies were collected at night and one during day; a chi-square test for goodness of fit ($\chi^2 = 6.4$, df = 1, $p < 0.01$) showed this difference was also statistically significant. No significant relationships were detected between larval round goby densities at the surface and depth, sea height, or water temperature ($p > 0.05$).
DISCUSSION

No round gobies were collected during 1999, and few were found in surface ichthyoplankton net tows at our Lake Michigan sites beginning in 2000, which demonstrates that round gobies were at the beginning of their colonization of the Muskegon site during our study and were actually low in abundance (Jude, unpublished trawling data). The habitat at our Lake Michigan sampling site is sand with little rugose structure (optimal habitat for round gobies—Jude and DeBoe 1996) anywhere besides a small sunken artificial reef west and the heavily rapped harbor walls about 2 km north of our site. Thus, collecting round goby larvae approximately 2 km away from the nearest spawning habitat at the surface only at night is evidence to suggest that this is a diel vertical migration which may be a dispersal strategy or predator avoidance/prey pursuit behavior for this species which would have evolved in their native range. In addition, all larval round gobies collected at the surface were 6.5–8.9 mm long, suggesting this may be the optimal size at which round gobies ascend to the surface at night, possibly due to energetic costs associated with fish lacking swim bladders remaining in the water column at night.

### TABLE 1. Dates, depths, total number, and density (number / 1,000 m$^3$) of larval round gobies collected in surface plankton net tows in eastern Lake Michigan off Muskegon, MI, during 2000-2002, and in western Lake Erie off Gibraltar and South Bass Island near Put-In-Bay, OH, during 2003 and 2005. Larval round gobies were also collected in surface, drift-net samples at the north and south branch mouths of the Muskegon River at Muskegon, MI, during 2004 and in bottom sled-tow samples in Lake Michigan off Muskegon, MI, during 2001. LE = Lake Erie, LM = Lake Michigan, MR = Muskegon River mouth, N = neuston net, O = 0.75-m diameter, 363-µm-mesh net (Lake Michigan and Muskegon Lake) or 0.75-m diameter, 500-µm-mesh net (Lake Erie), S = sled tow, 0.5-m diameter, 363-µm-mesh net (Lake Michigan) and D = drift net, 0.5-m diameter, 363-µm-mesh net (Muskegon River). All round gobies were collected at night, except those labeled with an asterisk under Date.

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<th>Date</th>
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<th>Depth (m)</th>
<th>Net</th>
<th>Mesh (µm)</th>
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Vertical Migration of Round Gobies

larger sizes (Czesny et al. 2005). Evidence for this was that in our 2005 Lake Erie tows, which were done during the day (two depths, times, and replicates), no round gobies were collected, while comparable night tows collected 167 fish. Round gobies have no swim bladder, thus are negatively buoyant, and we have observed larval and juvenile round gobies in aquaria that would swim to the surface, then drift downward, unable to maintain their position above bottom without exerting effort to remain in the water column. In addition, we had previously observed males guarding newly hatched round gobies, and so concluded they were benthic in existence, agreeing with Miller (1984). However, our data document that at least some 6.5–8.9-mm larvae must disperse from the nest early and swim to the surface at night, since we caught so many in this size range in our surface tows up to 9 m off the bottom on calm days.

Round goby larvae may utilize surface or near-surface currents as a dispersal mechanism during diel vertical migrations. Previous research suggested that adult male round gobies guarded eggs and larvae to the juvenile stage (Miller 1984), but we find this to be practically impossible for fish larvae at the surface. Larval forms of some marine goby species, such as the reef-dwelling, bridled goby (Coryphopterus glaucofraenum) (Forrester 1999) and Hawaiian amphidromous goby (Lentipes concolor) (Radtké et al. 2001), use currents for dispersal and settle to the bottom when they are over suitable habitat. Tubenose gobies, which were introduced in the Great Lakes about the same time as round gobies (Jude et al. 1992), also use currents as a dispersal mechanism (Zitek et al. 2004). Male sand gobies (Potmataschistus minutus) exhibit nest-guarding behavior until their larvae are about 3 mm (10 days old). The larvae are pelagic at first then become demersal at about 17 mm (Miller 1986). Other gobies exhibit diel vertical migration behavior (Schultz et al. 2003). Round gobies have not been known to exhibit early life history behavior similar to the aforementioned gobies until now. In laboratory experiments, Logachev and Mordvinov (1979) noted that activity levels for round goby larvae increased notably on the third day after hatching when they reached 6.0–6.2 mm total length; their swimming speed then was almost twice that of newly hatched larvae. Round goby larvae likely developed this behavior to elude their native benthic invertebrate predators in the Black Sea, mainly shrimps (Leander spp.), isopods (Idotea spp.), amphipods (Gammarus spp.), and barnacle nauplii (Logachev and Mordvinov 1979). This suggests any purposeful movement into the water column would likely occur a few days after hatching, and round gobies we collected were large enough to exhibit this behavior.

Round gobies were presumably transported to the Great Lakes via transoceanic freighters (Jude et al. 1992), then began to appear only at major Great Lakes ports, strongly suggesting freighters as vectors of transport. They were first reported in the St. Clair River in 1990 (Jude et al. 1992), then appeared in the Grand River (a major gravel-hauling port) in Lake Erie (R. Thoma, Ohio EPA, Twinsburg, OH, pers. comm.) around 1994, and then in Calumet Harbor in southern Lake Michigan in 1995 (Janssen and Jude 2001). Jude et al. (1995) predicted that Duluth Harbor in Lake Superior would be the next site they would colonize, which occurred in 1995 (UMSGP 1995). Dispersal was rapid, and there was no evidence of round gobies in

FIG. 2. Density of larval round gobies collected in diel, surface, neuston-net (1 m × 2 m, 500-µm-mesh) tows at 3- and 9-m depth contours in western Lake Erie off of Gibraltar Island near Put-In-Bay, OH, during June 2005. Eight samples each were collected during day and night (4 tows at each depth contour per diel period), totaling 16 larval fish samples.
areas between these major ports. This process by which an exotic species links with an existing transport system was termed “hub and spoke” by Carlton (1996). Jude et al. (1995) speculated that the mechanism of dispersal for round gobies might be laying eggs in crevices of the hull of ships, swimming in holes or cracks while a ship was in harbor (we have observed round gobies sitting on vertical walls of concrete conduits while sampling tributaries in the Great Lakes—see also Wonham et al. 2000), or juveniles or adults being pumped into ship ballast water tanks or attracted to ship grates (Hoese 1973, Carlton 1985) after unloading freight at a port. However, it appears from our larval fish data that larval round gobies, now the only life stage known to travel high in the water column, being pumped into ship ballast tanks may be a mechanism of dispersal both from the Black and Caspian seas, where they apparently originated (Dougherty et al. 1996), and within the Great Lakes. Abundant supplies of zooplankton are sometimes available in these ocean-going vessels (70,000 m\(^{-3}\)—Locke et al. 1993), which could provide food for larval round gobies. Evidence to support this contention is 1) presence of larvae of benthic fishes, including gobies and European flounder, in ballast water samples taken elsewhere (Wonham et al. 2000, Gollasch et al. 2002), and 2) round goby larvae we collected up in the water column, where freighters take in ballast water. Stepien and Tumee (2006) have found great genetic diversity in Great Lakes round goby populations, which could be explained by repeated introductions from freighters bringing new batches of round gobies into Great Lakes ports with existing populations. Since only larval round gobies are known to be present in the water column, ballast water transport of enough round gobies to establish viable populations is most likely for this stage, rather than the post-larval life stages.

Since freighters are now larger and have improved than before (Dawson 1973), water quality has improved in Great Lakes harbors (Minchin and Gollasch 1998), and ships exchange ballast water in harbors that provide excellent habitat for round gobies to spawn (Wickett and Corkum 1998) and their prey to thrive (e.g., dreissenid mussels) (French and Jude 2001), the likelihood of invasive species such as round gobies becoming established has increased (Ojaveer et al. 1998, Ricciardi and Rasmussen 1998). Current open ocean exchange programs to limit introduction of invasive species (Taylor et al. 2002) are not totally effective (Galil and Holsmann 2002), and within the Great Lakes, only ships operating in Michigan ports have legal restrictions related to ballast water. Based on our research, we believe the spread of round gobies in the Great Lakes could have been mitigated if freighters had taken on ballast water only near the surface during the day, particularly in May through September when round gobies spawn. Galil and Holsmann (2002) similarly recommended that ballast water be taken on during daylight hours to prevent uptake of zooplankton in ballast water. Future research should be directed toward studying the diel depth distribution and the early life histories of current and potential invasive species to better predict mechanisms of dispersal and likelihood of establishment in new areas.

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