

Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: diel vertical migration of early juvenile round goby

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Abstract The round goby, *Apollonia melanostoma*, a molluscivore specialist, was introduced to the Great Lakes in the early 1990s and rapidly expanded its distribution, especially in Lake Erie. Adult round goby morphology suggests low dispersal and migration potential due to the lack of a swim bladder and benthic life style. Given that the larval stage occurs inside the benthic egg, and juveniles have adult morphologies, it has been suspected that dispersal and invasion potential is low for early life stages also. However, we identified early juvenile round gobies in the nocturnal pelagic in Lake Erie and thus we conducted a sampling study to determine the extent to which this life stage uses the nocturnal pelagic. Replicate ichthyoplankton samples were collected at 3-h intervals (1900–0700 h) at three depths (2 m, 5 m, 8 m) in western Lake Erie (water depth = 10 m) in July and August 2002 and June 2006. Early juvenile round gobies (6–23 mm TL) were present almost exclusively in the nocturnal samples (2200 h, 0100 h, 0400 h) with peak densities approaching 60 individuals per 100 m³ of water sampled. Nocturnal density was also significantly greater at 8-m depth versus 2-m and only the smallest fish (6–8 mm TL) migrated to

the surface (2-m). Analyses of diet clearly demonstrated that these fish are foraging on plankton at night and thus may not be light limited for foraging in ship ballast tanks. In ships that take on thousands of tonnes of water for ballast, nocturnal ballasting could easily result in transport of thousands of young round gobies at a time. Additionally, within-lake dispersal at this lifestage is likely common and may facilitate downstream passage across barriers designed to limit range expansion.

Keywords Diel vertical migration · Dispersal · Great Lakes · Invasive species · Lake Erie · Round goby

Introduction

Biological invasion success is a function of several factors including propagule size (number of invaders), invasion frequency, attributes of the invader (fecundity, dispersal ability), as well as biotic and abiotic conditions between the source and invasion sites (species diversity, niche gaps, physical conditions) (Ricciardi and MacIsaac 2000; Vanderploeg et al. 2002). Invasion of the Great Lakes by zebra mussels, (*Dreissena polymorpha*), is an example in which biological attributes such as high fecundity, broad environmental tolerances, and rapid dispersal ability combined with human activities (e.g.,

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transportation via ballast water) and the absence of natural predators resulted in rapid colonization (Nalepa and Schloesser 1993). Given the ecological and economic importance of limiting exotic introductions (Mills et al. 1994), it is critical to understand the mechanisms influencing species persistence and population expansion, which ultimately result in successful exotic species introductions.

Dispersal of fish from natal sites frequently occurs at a young age (larvae) soon after egg hatching (Mora and Sale 2002), although adult migration is also common in pelagic fishes (Fuiman and Werner 2002). As a result of the relatively small size of larval fish and the physical characteristics of the aquatic environment, early life stage dispersal is generally considered to be a function of water movements, such as horizontal water currents and upwelling. Additionally, many fish are able to adjust buoyancy within the water column (vertical migrations) using their swim bladder and thus utilize water currents for dispersal throughout the aquatic landscape (Fuiman and Werner 2002). Understanding dispersal mechanisms of invading species is critical because these provide potential avenues for efforts to block invasions, such as ballast water technology and import inspection procedures (MacIsaac et al. 2002).

The Great Lakes have undergone a series of biological invasions that have strongly modified biological and ecological interactions within the system, such as a loss of bivalve biodiversity (Schloesser et al. 1996; Strayer 1999), increased habitat competition with native fishes (Dubs and Corkum 1996), and increased resources to the benthic community (Stewart et al. 1998). These invasions are a direct result of human manipulation of the environment (e.g., Welland Canal, lamprey introductions) or unintentional movement of species among isolated but similar ecosystems.

A recent successful invader in the Great Lakes, the round goby (*Apollonia melanostoma*), has rapidly colonized the Great Lakes. The round goby was initially discovered in the St. Clair River near Sarnia, Ontario in 1990 (Jude et al. 1992), in Lake Erie in 1993 (Charlebois et al. 1997), and can now be found in all of the Great Lakes. Rapid population expansion was not expected because the round goby (1) is a benthic fish not adapted for long distance swimming, (2) does not have a swim bladder to regulate buoyancy, and (3) does not have a true larval stage

(i.e., larval development occurs within the benthic egg; MacInnis and Corkum 2000; Moyle and Cech 2000). These life history characteristics would be expected to constrain dispersal and migration potential. However, the rapid colonization of the Great Lakes suggests round gobies utilize other mechanisms for effective dispersal.

The round goby is native to the Black and Caspian Sea areas and was probably introduced to the Great Lakes through transatlantic ballast water exchange, although the specific life stage for this introduction is not known (Charlebois et al. 1997). General life history characteristics include aggressive territoriality in adult males, repeated spawning sessions (May through August), and high fecundity (200–10,000 eggs per individual per season; Charlebois et al. 1997). Eggs are guarded from predation and environmental influences, such as siltation, by the male until hatching, resulting in up to 95% of the eggs hatching per nest (Charlebois et al. 1997). Although round gobies are found at a range of depths (0 to ≥ 40 m), some evidence suggests adults migrate to deeper water during winter months and return to shallow water areas in spring (Charlebois et al. 1997). This putative seasonal migration of round gobies may partially explain this species' rapid expansion in the Great Lakes; however, it is unlikely that these migrations are the lone mechanism driving their rapid range expansion. Recent observations of early juvenile round gobies in the nocturnal plankton (Miner, unpublished data; J. Hageman, pers. comm.) suggested early post-hatching juvenile round gobies are able to enter the pelagic water and may undergo water current dispersal.

The objectives of this study were to quantify the use of pelagic waters by early juvenile round gobies and address within lake water current dispersal capability.

Methods and materials

Nocturnal use of pelagic waters by early life stage round gobies was quantified at a site between South Bass and Middle Bass islands in the western basin of Lake Erie during July, August 2002 and June 2006. Ichthyoplankton samples were collected every 3 h, from 1900 to 0700 h by horizontal plankton net tows at three depths (2 m, 5 m, and 8 m) within the water

column, which was always ≥ 10 m deep. Sunrise and sunset during this period ranged from 0612 h to 0634 h and from 2041 h to 2103 h, respectfully; thus, both diurnal and nocturnal use of the plankton was determined with this sampling. The nocturnal period included samples collected at 2200 h, 0100 h, and 0400 h while the diurnal samples were collected at 1900 h and 0700 h. Four-minute tows were conducted by deploying and retrieving a 0.75-m diameter, 500- μ m mesh ichthyoplankton net towed at a rate of ≥ 1 m s⁻¹. Two replicate samples per depth and time were collected on each date. Depth regulation of the net was achieved using a diving plane and weights attached to the sampling gear. The tow rope angle, measured with a clinometer, and length of tow rope were used to attain the necessary depth. The volume of water sampled was estimated using a General Oceanics mechanical flowmeter (model 2030R) suspended within the ichthyoplankton net mouth. Samples were collected on three dates, July 17/18, July 25/26, and August 8/9 in 2002 and on three dates in June 2006 (June 7/8, June 20/21, and June 28/29). Collected organisms were preserved in ethanol (50%-final concentration) for future laboratory analysis.

Early juvenile round gobies were identified, counted, and measured (total length) using a stereomicroscope with a graduated ocular micrometer. These data were used to estimate the size-frequency of collected round gobies and mean abundance of round gobies in the pelagic (individuals per 100 m³ of water sampled). Total lengths for round gobies collected during 2002 sampling were analyzed using a χ^2 contingency table to test for independence of round goby total length and capture depth. Since preliminary analyses of round goby pelagic density suggested that the data violated the homogeneity of variance assumption necessary for parametric statistical analyses, all density data (+1) were log₁₀ transformed (Zar 1999). Early juvenile round goby density in the pelagic was expected to be extremely variable resulting from abiotic factors (i.e., weather, lunar cycles) and the goal of this work was to evaluate diel vertical migration of early juvenile round gobies; therefore, statistical analysis incorporated a complete randomized block design with sample date as a block variable, sample depth (2 m, 5 m, 8 m) and time (nocturnal vs. diurnal) as category variables in a multifactor ANOVA (General Linear Model procedure, SAS Version 9).

A possible reason for the use of the nocturnal pelagic by juvenile round gobies is to maximize growth rate via foraging. To determine if juvenile round gobies were foraging in the pelagic and if there was selectivity for particular zooplankton during this period, we collected depth and time-specific zooplankton samples during one collection period (i.e., 8–9 August 2002) using a Schindler-Patalas trap (60- μ m mesh, 24.5 l). Zooplankton abundance and planktonic round goby diet data were used to calculate Chesson's diet selectivity indices (Chesson 1978). This index quantifies diet selectivity by comparing the proportion of taxa in the environment to the proportion of the same taxa in the diet using the expression:

$$\alpha_i = (r_i/p_i) / \sum_{i=1}^n (r_i/p_i)$$

where r_i is the proportion of prey taxon i in an individual fish's diet, p_i is the proportion of prey taxon i in the environment, and n is the number of prey taxa in the environment.

Zooplankton abundance estimates (#/L) in the environment were determined by enumerating all zooplankton from subsamples. For each fish used in the diet selectivity analysis, the corresponding abundance of zooplankton prey was based on the average of the two replicate samples taken at that depth and time. Taxonomic groups included copepods (cyclopoid and calanoid copepods), nauplii (copepod nauplii), *Daphnia* spp. (*Daphnia retrocurva* and a few *Daphnia lumholtzi*), *Eubosmina coregoni*, dreissenid (bivalve) veligers, eggs that were likely dreissenid, rotifers, and other rare taxa (*Leptodora* sp., *Diaphanosoma* sp., and ostracods). Diet analysis consisted of identifying all prey items from 50 juvenile round gobies (6.4–20-mm TL) collected on 8–9 August and determining the proportion of each taxon in each fish's diet. Mean and 95% CI for diet selectivity were then determined for each zooplankton taxon. Positive selectivity for a particular prey taxon occurred when mean selectivity and 95% CI were greater than the estimate for neutral selectivity (i.e., $1/n$, where n = number of prey taxa = 7). Similarly, negative selectivity for prey occurred when the mean value and 95% CI were less than $1/n$. Fish with empty stomachs ($n = 12$) were not included in the analysis.

Results

Distribution

Pelagic early juvenile round gobies (<23-mm TL) were collected almost exclusively in the three nocturnal sample times (2200 h, 0100 h, 0400 h) during the six sampling dates (Fig. 1). Only seven round gobies were collected during the two diurnal sampling periods (1900 h and 0700 h) representing only 0.5% of the round gobies collected ($n = 1503$ total, both years). Although early juvenile round goby density was variable when compared across all sampling dates, all days had a characteristic peak of pelagic

round gobies occurring during nocturnal sampling with densities declining to zero during diurnal periods (Fig. 1). Peak round goby densities ranged from 60 individuals per 100 m^3 at 8-m deep on July 17/18 to 6.5 individuals per 100 m^3 on June 7/8 (5-m deep). Of the >1500 fish collected, 23%, 34%, and 43% were caught at 2-m, 5-m and 8-m depth, respectively.

Pelagic round goby density varied significantly by sampling time (i.e., diurnal vs nocturnal) and sampling depth, while the time-by-depth interaction was not statistically significant (ANOVA, Table 1, $P < 0.05$). Tukey post-hoc comparisons of sampling depth indicate statistically higher densities of round gobies collected at 8-m than at 2-m (no differences by

Fig. 1 Pelagic juvenile round goby density for six sampling dates in western Lake Erie. Filled circles indicate density at 2-m depth; open circles = 5-m depth; triangles = 8-m depth. Fish were collected with an ichthyoplankton net at 2 m, 5 m, and 8 m depth in water ≥ 10 -m deep. Means (and ± 1 standard error) are based on two replicate samples ($\log_{10}(\text{density} + 1)$ transformation). Nocturnal samples were collected at 2200 h, 0100 h, and 0400 h. *Note:* no data collected on 7/18/02 at 0400 h, 6/20/06 at 0700 h, and 6/28/06 at 1900 h and differences in scale for all sampling dates

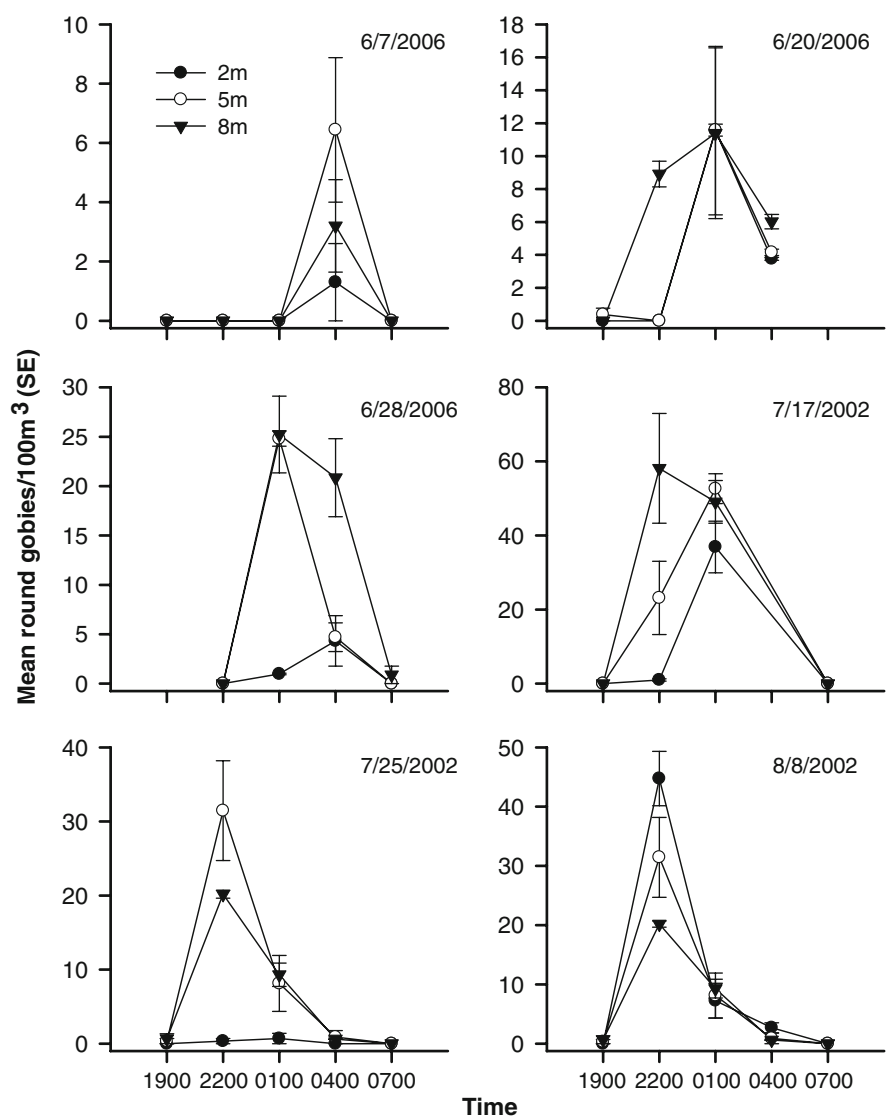


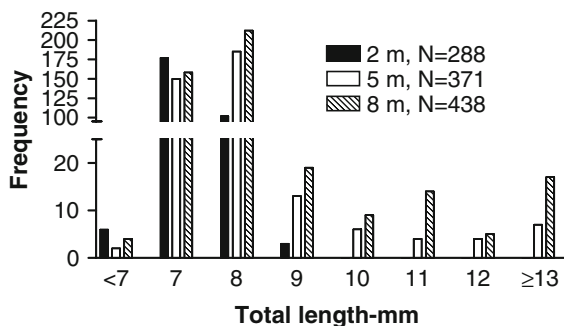
Table 1 Multiple-factor ANOVA for the abundance of pelagic juvenile round gobies on three sampling dates in 2002 and three dates in 2006 in western Lake Erie

Treatment	df	MS	F	P
Time (T)	1	95.57	86.48	<0.0001
Depth (D)	2	3.71	3.36	0.0371
D × T	2	0.54	0.49	0.6137
Error	172	1.11		

Date was used as a blocking variable. Fish were collected with an ichthyoplankton net at five times (1900 h, 2200 h, 0100 h, 0400 h, and 0700 h) at 3 depths (2 m, 5 m, 8 m) in water ≥ 10 m deep. Times were classified as nocturnal (2200 h, 0100 h, 0400 h) or diurnal (1900 h, 0700 h) for analysis

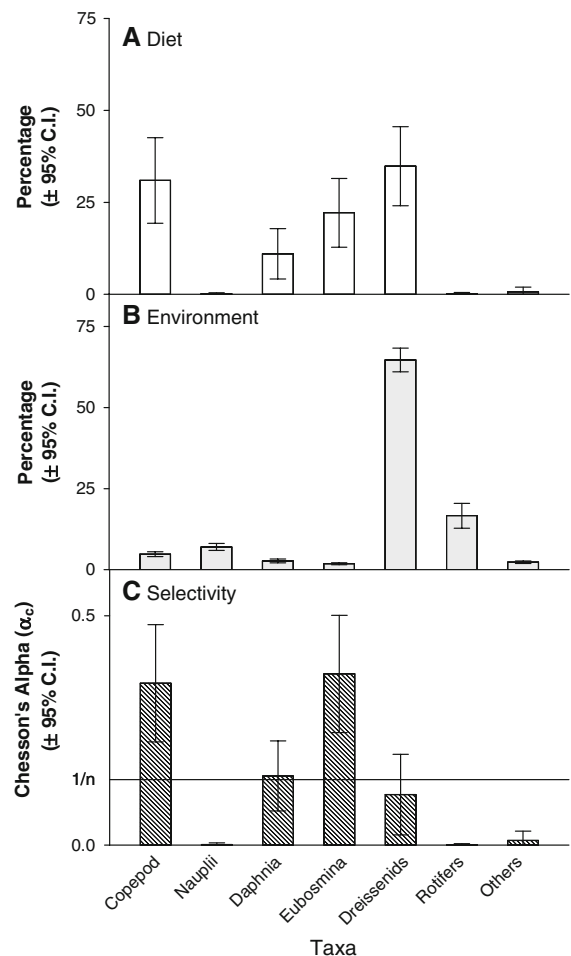
depth with 5-m). The significant depth effect suggests individuals do not distribute randomly throughout the water column. Additionally, round goby abundance in the nocturnal pelagic was significantly greater than abundance during diurnal periods (1900 h and 0700 h, i.e., a time effect, Fig. 1).

A size-dependent depth distribution of pelagic round gobies was clear in the nocturnal samples collected in 2002 (not addressed with 2006 data). Individuals ≥ 10 -mm TL were found only in 5- and 8-m deep samples, while individuals < 10 -mm TL were found at all sample depths (Fig. 2, $\chi^2 = 80.57$, $df = 14$, $P < 0.0001$). Overall, length of individuals ranged from 5.6-mm total length (TL) to 23-mm TL with a median length of 8.0-mm TL. Maximum length of individuals captured at the 2, 5, and 8-m depths were 9.4-mm TL, 20.0-mm TL, and 23.0-mm TL, respectively (Fig. 2).

**Fig. 2** Length–frequency distribution by collection depth of pelagic juvenile round gobies in western Lake Erie. Chi-square analysis consisted of 1-mm length classes and the class ≥ 13 -mm TL. $n = 1097$. Fish collected over three sample dates in 2002 were pooled

Diet and selectivity

Early juvenile round goby diet in August consisted primarily of four pelagic taxa. Numerically, dreissenids (eggs and veligers) comprised 35% of round goby diets, while copepods comprised 31% of the diet (Fig. 3a). *Eubosmina coregoni* and *Daphnia retrocurva* represented 22% and 11% of the diet, respectively (Fig. 3a). Rotifers, copepod nauplii, and miscellaneous taxa, such as *Leptodora kindti*, *Diaphanosoma* sp. and ostracods occurred infrequently in the diet, less than 1% combined (Fig. 3a). Zooplankton in the environment was numerically dominated by *Dreissena* veligers and eggs (mean = 64.6%,

**Fig. 3** Diet analysis of nocturnal juvenile round gobies collected in the pelagic of western Lake Erie. (a) Percentage of taxa in diet (mean $\pm$ 95% CI), (b) percentage of taxa in environment (mean $\pm$ 95% CI), and (c) diet selectivity (α) (mean $\pm$ 95% CI)

145 organisms l^{-1}) and rotifers (mean = 16.6%) (Fig. 3b), while no other taxon accounted for more than 10% of the zooplankton in Lake Erie at this location (Fig. 3b).

Early juvenile round gobies exhibited strong positive diet selection for copepods and *Eubosmina coregoni* (Fig. 3c). All other taxa had mean selectivity and 95% CI values less than or equal to $1/n$, indicating negative or neutral selectivity (Fig. 3c). These results clearly demonstrate that planktonic juvenile round gobies feed in the nocturnal pelagic, and are not simply utilizing the pelagic water currents as a mechanism of dispersal. The extent to which this nocturnal planktonic foraging supplements diurnal benthic consumption is not known.

Discussion

Results of this study confirm that early juvenile round gobies undergo diel vertical migrations in Lake Erie. In a similar study, density of early juvenile round gobies were quantified in the surface waters of a Lake Michigan estuary and Lake Erie (Hensler and Jude 2007). Although results are similar between these studies and suggest early juvenile round gobies undergo diel vertical migrations, Hensler and Jude (2007) reported lower round goby densities than observed in this study at a similar sampling location in western Lake Erie. In our study, horizontal tows were collected at 2, 5, and 8-m depths and suggest a significant non-random vertical distribution of early juvenile round gobies with generally higher densities at the 8-m sampling depth. In comparison, Hensler and Jude (2007) only conducted surface tows and did not quantify early juvenile round goby density at different depths in the water column. As such, differences between round goby density estimates of these two studies may be explained by depth-dependent vertical migrations, abiotic factors such as weather and lunar cycles influencing vertical migration, or more likely, a combination of abiotic and biotic factors regulating vertical migration.

Previous research into the life history of round gobies (Charlebois et al. 1997; Charlebois et al. 2001) and its likely mechanism for dispersal and invasion of new habitat has not identified the use of the pelagic by early juveniles. A planktonic life stage is a common characteristic of aquatic taxa with a high

potential for invasion (Ricciardi and Rasmussen 1998; Vanderploeg et al. 2002) and the results of this study demonstrate the potential planktonic abundance and nocturnal distribution of early juvenile round gobies.

Diel vertical migration by aquatic organisms is well established, (Hutchinson 1967; Wright et al. 1980; Neilson and Perry 1990) although, factors that drive and regulate vertical migration of fishes are thought to vary widely (Brett 1971; Hall et al. 1979). Vertical migration by larval fishes may be (1) an adaptive strategy for thermoregulation of resource processing (i.e., digestive, metabolism; Brett 1971; Wurtsbaugh and Neverman 1988), (2) a mechanism for predator avoidance (Eggers 1978), (3) a strategy to maximize foraging success (Janssen and Brandt 1980) or (4) a combination of these hypotheses (i.e., predator avoidance-foraging hypothesis; Clark and Levy 1988). Given that Lake Erie is generally isothermal to depths of 10–11 m, it is unlikely that the adaptive significance of vertical migration by early juvenile round gobies can be explained by thermoregulation. The predator avoidance hypothesis suggests predation risk is partially dependent on detection ability by the predator, and thus, predation risk may be reduced at times with low light intensity (Clark and Levy 1988; Appenzeller and Leggett 1995). Thus, round gobies may enter the pelagic water only at night when visual predators are light limited and remain close to the substrate during diurnal periods while predators are actively foraging. In our study, >99% of the juvenile round gobies collected in the pelagic were obtained during the nocturnal period. Although we do not know the percentage of the overall juvenile round goby population that vertically migrates, it is clear that mass vertical migration during nocturnal periods is occurring, given the densities observed. In conjunction with predator avoidance, vertical migration may facilitate planktonic feeding (Clark and Levy 1988). If early juvenile round gobies were not feeding in the nocturnal pelagic, we would expect to find few individuals with prey items in the diet or prey items not distributed uniformly throughout the gut. However, our analyses suggest pelagic zooplankton prey were present throughout the water column as well as uniformly distributed throughout the gut. In general, actively feeding larval and juvenile fish have short gut evacuation times that decrease with increasing

water temperatures (Persson 1979; Mills et al. 1984; Pedersen 1984). Therefore, prey items consumed by early juvenile round gobies during benthic periods were presumably evacuated from the gut before entering the nocturnal pelagic because they were not reflected in our diet analyses. Although we cannot definitively say that these fish were foraging in the pelagic, our results suggest it is likely. Additionally, our attempts to age these individuals were unsuccessful because we could not identify daily increments on otoliths. Daily otolith increment formation in larval and juvenile fish may be a function of feeding periodicity resulting from fish unable to effectively forage during nocturnal periods and undergoing a period of starvation (Campana and Neilson 1985). Therefore, if early juvenile round gobies do effectively forage throughout the diurnal and nocturnal periods, daily otolith increments may not develop.

Given the importance of rapid growth on survival, nocturnal vertical migration may be an adaptive strategy to minimize predation risk and maximize foraging/growth success. Jude et al. (1995) have shown that round gobies, with their exposed neuro-masts, are better able to capture nocturnal zooplankton than indigenous mottled sculpins, *Cottus bairdi*, which raises the question why juvenile round gobies are migrating into the pelagic when benthic resources available during the day should also be accessible at night. Clearly, exploring the predation risk-growth rate tradeoff between diurnal and nocturnal periods in the benthos versus the pelagic is needed (Werner et al. 1983; Anholt and Werner 1995).

Size-frequency distributions of planktonic round gobies varied significantly by sample depth. This may indicate decreasing benefits (or increasing costs) for juvenile round gobies entering the nocturnal water column as length increases. Individuals ≥ 10 -mm TL were only captured at 5- or 8-m depth and not in surface waters (2-m depth). Energy expenditure by round gobies to enter and maintain location within the nocturnal pelagic, in addition to increased risk of predation (resulting from increased size) must be offset by the energetic gains of feeding on pelagic zooplankton; this appears to occur when these fish are small, but the trade-off advantage appears to be lost rapidly as they increase in size. Ontogenetic habitat shifts similar to this are common (e.g., bluegill, *Lepomis macrochirus*, Werner and Hall 1988).

Another potential explanation for size-dependent vertical migration is that individuals ≥ 10 -mm TL may be less gape limited for benthic prey, therefore lowering the benefits to entering the nocturnal pelagic.

Logachev and Mordvinov (1979) suggest that round gobies are active and able to swim immediately following hatching and rapidly improve swimming ability. Newly hatched round gobies are active 7% of the time and have an average swimming rate of 2 cm s^{-1} , while three-day old round gobies are active 29% of the time and are able to swim 4 cm s^{-1} . Given these results, early juvenile round gobies may be able to enter the pelagic water by swimming and are not constrained to the benthos by the lack of a swim bladder. Similarly, the pelagic lifestage of marine gobies in the family Gobiidae is well documented (Sponaugle and Cowen 1994; Kingsford 2001; Radtke et al. 2001; McIlwain 2003). Clearly, a better understanding of swimming ability for this life stage is needed, as well as factors regulating use of the pelagic.

Prevailing hypotheses suggest that adult round gobies were entrained in ballast tanks and transported to Lake Erie. However, our results demonstrate that early juvenile round gobies are able to enter the nocturnal pelagic and thus high densities of this life stage may have been entrained in ballast tanks and released in Lake Erie and at harbors throughout the Great Lakes and Europe. Modern ships with high capacity ballast tanks could easily provide substantial propagule size (i.e., number of new colonists in a single invasion event) to increase the likelihood of establishment (Groves and Burdon 1986; Ricciardi and Rasmussen 1998). In our study, the highest abundance in the pelagic was $60 \text{ individuals m}^{-3}$. Therefore, a ballast water uptake of $10,000 \text{ m}^3$ with juvenile round gobies at this density could result in approximately 600,000 individuals entrained in the ballast water. Furthermore, because adult round goby densities are highest in the cobble/riprap substrates common around harbors (Ray and Corkum 2001), densities of planktonic juvenile round gobies may be even higher where ballast tank filling occurs. Certainly, the hypothesis of a small founding population in the Great Lakes is not supported by genetic studies, as genetic variability of the round goby is similar between European and Great Lakes populations (Dougherty et al. 1996; Dillon and Stepien 2001).

In addition to being the most likely source of transatlantic dispersal, early juvenile use of the nocturnal planktonic may contribute strongly to intra-lake dispersal of round gobies. As an exercise to estimate potential dispersal distances of early juvenile round gobies, time spent in the pelagic was multiplied by an estimate of water current velocity. Given the results of our pelagic sampling, juvenile round gobies appear to spend as much as 6 h per night in the pelagic (although we could not track individuals). Mean summer current velocity estimates in Lake Erie range from 0.1 to 4.4 cm s⁻¹ (Kovacik 1972; Beletsky et al. 1999). Combining these variables suggests early juvenile round goby dispersal ability for a 6-h pelagic night is about 1 km. In this example, seasonal mean current velocities were used to estimate dispersal ability. Therefore, high velocity water currents resulting from extreme weather may result in substantial variability in dispersal ability. This example does not suggest dispersal direction, or take into consideration the ability of early juvenile round gobies to direct dispersal outcome through swimming; however it does illustrate the likely importance of early life stage drift dispersal in population expansion within the Great Lakes.

The ‘invasional meltdown’ hypothesis suggests ecosystems become less invasion resistant with increasing species diversity (Simberloff and Von Holle 1999; Ricciardi 2001). This hypothesis suggests perturbations of the community by previous successful invasions may facilitate future invasions by creating and modifying existing niches, effectively opening the door to invaders adapted to those niches (Simberloff and Von Holle 1999). In the Great Lakes, the establishment of the zebra mussel (*Dreissena polymorpha*), an important prey for the round goby, may have facilitated the subsequent establishment of the round goby by providing an unexploited food resource (Charlebois et al. 1997; Simonovic et al. 2001). The Great Lakes may be undergoing an ‘invasional meltdown’ and are likely to experience future successful invasions (Ricciardi 2001). Therefore, it is critical to identify all invading species dispersal mechanisms and understand how those mechanisms regulate successful species introductions. It seems unlikely that the round goby invaded successfully from just a few adults in ballast water. Instead, even a single introduction of thousands of early juveniles at multiple locations may have been

the lifestage and propagule size necessary to ‘seed’ the Great Lakes.

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