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Population Structure of the Invasive Round Goby in Lake Michigan

Elizabeth A. LaRue *Grand Valley State University*, laruee@mail.gvsu.edu

Carl Ruetz III *Grand Valley State University*, ruetzc@gvsu.edu

Ryan Thum *Grand Valley State University*, thumr@gvsu.edu

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Undergraduate Research and Creative Practice

Student Summer Scholars

Grand Valley State University Year 2009

Population Structure of the Invasive Round Goby in Lake Michigan

Elizabeth A. LaRue* Carl R. Ruetz III** Ryan A. Thum†

* Grand Valley State University, laruee@mail.gvsu.edu ** Grand Valley State University, ruetzc@gvsu.edu † Grand Valley State University, thumr@gvsu.edu

Abstract

The recent establishment of the round goby (*Neogobius melanostomus*), an invasive fish in Lake Michigan, provides a model system to view fine scale evolutionary and ecological processes that can create genetic structure within a population. We used seven nuclear polymorphic microsatellite markers ($N = 11-17$ per site) and measurements of fish total length, weight, and sex ($N = 20-74$ per site) on round gobies captured by minnow traps and angling among 12 sites around the entire shore of Lake Michigan to determine if evolutionary processes are present in Lake Michigan by characterizing population structure of the round goby. Specific objectives were to determine whether: 1) there are significant patterns of genetic population structure among sites along the shore of Lake Michigan (e.g., a correlation between genetic diversity and geographic distance), 2) ferry shipping routes create strong deviations from normal population structure observed to occur around the lakeshore, and 3) density, fish size, and condition at the 12 sites differ from each other. Results include: significant pairwise F_{ST} values, a pattern of isolation by distance (IBD) along the eastern and western shores of Lake Michigan, no IBD along the entire lakeshore, northern, or southern shores, different catch per unit effort (CPUE) and mean weight between sites. A length/weight relationship between fish at all 12 sites was not different. Results indicate that round goby pierhead sites exhibit population structure in Lake Michigan.

Introduction

Ecological and evolutionary factors that hinder or facilitate the range expansion of species are of fundamental interest to evolutionary ecologists. Invasive species offer unique opportunities to study the evolutionary ecology of range expansions (Hanfling 2007, Lee 2002, Sax et al. 2007, Suarez and Tsutsui 2008). A focus of invasion biology is to understand what factors cause an invasion to be so successful. Exposure to novel environmental factors during range expansion can cause many ecological and evolutionary changes to population structure (Hanfling 2007, Lee 2002, Sax et al. 2007, Suzrez and Tsutsui 2008). These changes may give an indication of reasons behind the relative success of a range expansion (Lee 2002).

The evolutionary potential of invasive species is another major focus of invasion biology. A species' evolutionary potential represents the adaptive and nonadaptive processes that may explain why some species invade new ranges so well (Chun et al. 2009). Adaptive processes are changes in heritable (genetically based) traits via natural selection that increase survival and fecundity. Nonadaptive processes are changes in traits via processes other than natural selection (Chun et al. 2009). For example, genetic isolation, or a lack of gene flow, among subpopulations may cause genetic differentiation by random change (i.e., genetic drift). Genetic drift is accelerated by founder effects and demographic bottlenecks, both of which may be frequently experienced in range expansions (Stepien et al. 2005).

The presence of evolutionary processes may be tested by the use of genetic markers to determine genetic population structure (Le Roux and Wieczorek 2009). For example, microsatellites (tandem repeats of nucleotides within the genomic sequence) can be used to calculate measures of neutral genetic variation between subpopulations. This allows us to answer whether invasive species consist of ecologically and/or evolutionarily distinct versus homogeneous collections of subpopulations. We then can infer whether evolutionary processes

are present in a species invasive range, which is the first step to determine if evolutionary potential has facilitated range expansion.

We are using the invasive round goby (*Neogobius melanostomus*) in Lake Michigan to study the evolutionary potential of invasive species. The round goby is an ideal species to study evolutionary ecology of range expansions, because it was recently discovered in the St. Claire River in 1990. The round goby was most likely transported to the Great Lakes by ship ballast water uptake of vertically migrating larval fish (Hensler and Jude 2007, Hayden and Miner 2008). Brown and Stepien (2009) determined that the round goby source population originated from the mouth of the southern Dnieper River in Kherson, Ukraine, a major Black Sea port by the use of mitochondrial cytochrome b gene sequences and seven nuclear microsatellites. The round goby has also been very successful. The invasion of the five Great Lakes occurred within 10 years of its first discovery.

Both ecological and evolutionary hypotheses have been proposed to explain the great success of the round goby in the Great Lakes. Ecologically, tolerance to a wide range of environmental factors such as being able to survive in marine and freshwater habitats (Jude et al. 1992) and thermal tolerance (Cross and Rawding 2009) may have facilitated this fish's invasion. The invasion of a native food source, the zebra mussel (*Dreissena polymorpha*), may have also have helped the round goby (Bauer et al. 2007, Stepien et al. 2005). Evolutionarily, it has been hypothesized that by multiple founding sources and the absence of founder effects, which would be a cause of high genetic diversity in the invasive population, may facilitate invasive success (Brown and Stepien 2009, Brown and Stepien 2008, Dillon and Stepien 2001, Dougherty et al. 1996, Stepien and Tumeo 2006, Stepien et al. 2005). Multiple founding sources could create new genotypic combinations allowing for selection of the most adaptive phenotype in a novel environment. It has been found that in a comparison of genetic differentiation between populations from the native and invasive ranges, that genetic diversity was similar (Brown and Stepien 2009, Brown and Stepien 2008). This is also true for other Ponto-Caspian invaders to the Great Lakes such as the Eurasian ruffe (*Gymnocephalus cernuus*), zebra mussel, and tubenose goby (*Proterorhinus semilunaris*) (Stepien et al. 2005).

The objective of our study was to characterize round goby population structure in genetics, density, size, and fish condition to determine if evolutionary processes are present in Lake Michigan. Specific objectives were to determine whether: 1) there are significant patterns of genetic population structure among sites along the shore of Lake Michigan (e.g., a correlation between genetic diversity and geographic distance), 2) ferry shipping routes create strong deviations from normal population structure observed to occur around the lakeshore, and 3) density, fish size, and condition at the 12 locations differ from each other.

Methods Data Collection

We collected round gobies by baited minnow traps and angling in rocky substrate from 12 pierhead locations around the lakeshore of Lake Michigan between May 26 to July, 1 2009 (Fig. 1). Round gobies tend to prefer rocky substrate (Ray and Corkum 2001, Taraborelli et al. 2009). Minnow traps were found to be an effective method for round goby capture in middle to late summer by Diana et al. (2006). Traps were set in the evening baited with approximately 0.20 lb

of chicken liver and pulled in the morning. Mean average soak time ranged from 12.72 hr ($SE =$ 0.045) in Holland, MI to 20.59 hr ($SE = 0.283$) in Chicago, IL.

Total length, weight, and sex was recorded for 20-74 fish per site. Caudal fins were removed from 20-52 fish per site and stored individually in 95% ethanol for genetic analysis.

Fig. 1. Pierhead sites in Lake Michigan.

DNA Extraction and Amplification

Genomic DNA was extracted from caudal fin tissue with Qiagen DNeasy 96 kits for 11-17 individuals per site ($N_{total} = 186$) and stored at -20.0 °C.

Eight polymorphic nuclear microsatellite loci from Dufour et al. (2007) were amplified by polymerase chain reaction (PCR). We used a 10 µL PCR reaction mixture that contained 5X taq buffer (Promega), 2.5 mM $MgCl₂$, 0.2 mM dNTPs, 0.2 µM of each fluorescent microsatellite primer (Dufour et al. 2007), 1.0 U taq polymerase (PROMEGA), and template with an oil overlay to guarantee constant volume. Amplification was performed on a EPgradient S Mastercycler (eppendorf) with an initial 120 s denaturation at 94 °C, followed by 10 cycles of 94 °C with 15 s annealing at 55 °C, and a 15 s 72 °C extension, followed by 30 cycles of 94 °C and annealing at 48 °C. Microsatellite amplification products were then separated into two plates and send to the University of Illinois for fragment analysis. The first plate consisted of Nme 1, Nme

2, Nme 4, Nme 5, and Nme 7 with PCR products diluted 1:20 for Nme 1, 2, 4 and 1:50 for Nme 5 and 7. The second plate consisted of Nme 3, Nme 8, and Nme 9 with a 1:20 dilution.

Genetic Analysis

Raw data was scored in GENEMAPPER for allele size and then visually inspected. We excluded Nme 6 and 10 from our analysis due to scoring abnormalities. Null alleles and large allelic dropout that can cause significant deviation from Hardy-Weinberg Equilibrium was checked for by MICROCHECKER version 3.23 (Van Oosterhout et al. 2004). Nme 7 was found to significantly deviate from Hardy-Weinberg Equilibrium due to the possible presence of null alleles. We excluded Nme 7 from analysis. Linkage disequilibrium was calculated by ARLEQUIN 3.1 (Excoffier et al. 2005) to determine if association of pairs of alleles at two loci were nonrandom. No physical linkage between pairs of loci was discerned.

Table 1. Microsatellite markers (Dufour et al. 2007). Number of alleles (N_A), allelic range (base pairs), repeat motif, observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficent (F_{IS}) for round gobies collected at 12 sites in Lake

Microsatellite N_A		Allelic Range (bp)	Repeat Motif	H _o	H_E	F_{IS}
Nme 1	16	252-368	(GTCA)8(GTCT)11GC(CTGT)10	11.83	11.14	0.018
Nme ₂	$\overline{4}$	238-249	(CA)13	4.75	4.82	0.027
Nme 3	9	135-187	(AGAC)14	9.89	9.33	0.065
Nme 4	3	107-124	(TCTG)7	7.58	7.15	-0.08
Nme 5	6	134-149	(CA)4GC(TCTG)7	$\overline{2}$	2.68	-0.016
Nme 8	8	281-292	(TG)8	12	11.19	-0.064
Nme 9	7	168-220	(ATCC)12	8.42	8.64	0.006
		*Nme 5 was momomorphic for 5 sites.				

Average allelic frequency and conformations to Hardy-Weinberg equilibrium were calculated by GENEPOP version 3.4 (Raymond and Rousset 1995). AMOVA in ARLEQUIN 3.1 was used to explain genetic variation partitioned among and within populations. F-statistics were used to determine if significant population structure was exhibited in the twelve sites from Lake Michigan. Pairwise F_{ST} values and significance after sequential Bonfferoni corrections (Rice 1989) with 1,023 permutations was calculated by ARLEQUIN 3.1. A Mantel test by ARELQUIN 3.1 was performed to determine if pairwise F_{ST} values and geographic distance were related in a pattern of isolation by distance. Geographic distance was calculated as the shortest distance between sites along the lakeshore.

Genetic differentiation between sites directly across the eastern and western lake shores of Lake Michigan were compared for deviations from the observed isolation by distance pattern. Pairwise F_{ST} values were compared for significance between Muskegon, MI and Milwaukee, WI and Ludington, MI and Manitowoc, WI, Both pairs of sites are connected by daily cross lake ferry transport (Lake Express, SS Badger).

Demography, Size, and Condition

Analysis of variance (ANOVA) was used to determine differences in mean catch per unit effort (CPUE) and mean weight of fish captured in minnow traps between pairwise comparisons of sites. Variance explained by linear regression in a total length/weight relationship of all fish captured by minnow traps was determined by ANOVA. Significance was determined after Tukey-Kramer corrections.

Results Genetic Diversity

Seven microsatellite markers were amplified for 12 sites in Lake Michigan $(N = 11-17)$ (Table 2). We found all loci at all sites to be polymorphic except for Nme 5, which was monomorphic for five locations. The average number of alleles per loci at each site ranged from 3.14-5.14 (Table 2). Populations did not deviate significantly from Hardy-Weinberg Equilibrium, because expected heterozygosity did not deviate significantly from expected heterozygosity (Table 2).

Table 2. Locations, sample size (N), average number of alleles (Average N_A) observed heterozygosity (H_O),

expected heterozygosity (H_E), average inbreeding

coeffiecent (Average F_{IS}) for round goby subpopulations in **Lake Michigan.**

Genetic Differentiation

AMOVA determined that 5.31% of genetic variation was found among populations ($P =$ \leq 0.001) and 94.69% of genetic variation was found within populations (P = \leq 0.001) (Table 3).

Pairwise F_{ST} values found a range of population differentiation levels between sites. Values ranged from -0.018 to 0.155 (Table 4). Out of 65 pairwise comparisons, 23 were significant after sequential Bonferonni corrections (Table 4). The greatest difference was between St. Ignace and Holland at 0.155. The smallest degree of difference was between Chicago and Escanaba at -0.018. St. Ignace had the most significant pairwise F_{ST} comparisons of all 12 sites (10 of 11).

Table 4. Pairwise F_{ST} values of 12 round goby pierheads in Lake Michigan with significant values after sequential Bonferonni corrections bolded $(a < 0.05)$.

	SJ	HO	MU	LU	FR	CA	SI	ES	MA	MI	KE
Holland	0.032										
Muskegon	0.033	0.012									
Ludington	0.034	0.038	0.026								
Frankfort	0.047	0.089	0.045	0.025							
Charlevoix	0.0008	0.072	0.034	0.007	0.006						
St. Ignace	0.117	0.155	0.073	0.088	$0.085 \mid 0.081$						
Escanaba	0.008	0.044	0.028	0.038	0.032	0.014	0.146				
Manitowoc	0.1	0.128	0.063	0.056	0.04	0.053	0.042	0.100			
Milwaukee	0.037	0.04	-0.02	0.015	0.029	0.026	0.054	0.028	0.037		
Kenosha	0.015	0.078	0.053	0.061	0.064	0.02	0.084	0.041	0.073	0.046	
Chicago	0.018	0.061	0.052	0.042	0.05	0.023		0.153 - 0.018 0.140 0.044 0.052			

We used a Mantel test to determine if a correlation between pairwise F_{ST} and geographic distance was present between sites around the lakeshore of Lake Michigan (Fig. 2.a). No isolation by distance (IBD) pattern was observed (Mantel = 0.0058 , P = 0.453). A Mantel test did find a pattern of IBD along the eastern shore of Lake Michigan from St. Joseph to St. Ignace (Mantel $= 0.56$, $P = 0.007$) (Fig. 2.b) and along the western lake shore from Chicago to Manitowoc (Mantel = 0.83 , P = 0.028) (Fig. 2.c). No IBD pattern was found along the northern lake shore from Escanaba to Frankfort (Mantel = -0.18 , P = 0.56) (Fig. 2.d) or the southern lakeshore from Milwaukee to Muskegon (Mantel = -0.04 , P = 0.56) (Fig. 2.e). When the outlier comparison between Milwaukee and Muskegon (distance = 633.88 km, F_{ST} = -0.015) is removed the linear regression between sites on the southern lakeshore shows a stronger positive correlation between pairwise F_{ST} and geographic distance (Fig. 2.f).

Fig. 2. Correlation between pairwise F_{ST} values and geographic distance in Lake Michigan along a) 12 sites (Mantel = 0.0058 , P = 0.453), b) the eastern lakeshore (St. Joseph to St. Ignace) of Lake Michigan (Mantel = 0.56 , P = 0.007), c) the western lakeshore (Chicago to Manitowoc) of Lake Michigan (Mantel = 0.83 , P= 0.028), d) the northern lakeshore (Frankfort to Escanaba) of Lake Michigan (Mantel = -0.18 , P=0.56), e) the southern lakeshore (Muskegon to Milwaukee) of Lake Michigan (Mantel = -0.04, P $= 0.56$), f) the southern lakeshore (Muskegon to Milwaukee) of Lake Michigan minus pairwise comparison between sites Muskegon and Milwaukee.

A comparison between sites directly across Lake Michigan and connected by passenger ferry transport showed conflicting relationships. The pairwise F_{ST} between Muskegon and Milwaukee was not significant at -0.015 (Table 4). This indicates transport of round gobies between the two locations is potentially strong by the Lake Ferry Express. Ludington and Manitowoc had a significant pairwise F_{ST} of 0.056 (Table 4) indicating that transport of round gobies may not be extensive by the SS Badger.

Demography, Size, and Condition

A total of 1,388 round gobies were captured at 12 sites in Lake Michigan. A total of 1,314 round gobies were captured by minnow traps from the 12 pier head locations in Lake Michigan. The highest mean CPUE was 34.69 fish per trap ($SE = 3.203$) in Chicago, IL and the lowest 0.14 (SE = 0.097) in Escanaba, MI (Fig. 3). The mean CPUE at each site was significantly different between pairwise comparisons of locations by ANOVA (39 out 66 comparisons significant).

Fig. 3. Mean catch per unit effort (CPUE) of minnow traps at 12 pierheads in Lake Michigan (ANOVA: $F_{11,160} = 26.8$, p<0.001). CPUE significantly different for 39 of 66 pairwise population comparisons. Error bars \pm 1 SE.

Weight was taken for a total of 571 fish captured by minnow traps at each of the twelve sites. Mean weight of fish caught in minnow traps ranged from 4.26 g (SE = 0.329) in St. Ignace, MI to 18.91 g ($SE = 1.10466$) in Kenosha, WI (Fig.4). The mean weight of fish caught at each site was significantly different for 36 out of 66 pairwise comparisons by ANOVA.

Fig. 4. Size of round gobies captured by minnow traps at 12 pierheads in Lake Michigan (ANOVA: F_{11, 633} = 52.49, p<0.001). Weight differed significantly for 36 of 66 pairwise population comparisons. Error bars \pm 1 SE.

A relationship between the Log_{10} total length and Log_{10} weight for all fish captured by minnow traps for all sites produced a linear regression of $y = 3.18482x - 2.03463$ (p<0.0001) (Fig. 5). Linear regression explained 96.74% of the variation in the dataset (adjusted R^2 = 0.9674). As an indicator of fish health a length/weight relationship slope over three indicates a fish weighs more than its length and a value below three indicates that a fish is longer than its weight.

Fig. 5. Relationship between length and weight of round gobies captured by minnow traps at all sites in Lake Michigan ($N = 644$).

Discussion Genetic Diversity

AMOVA determined that hierarchal genetic variation was low among populations (5.31%) and was explained mostly by within population genetic variation (94.69%) (Table 3). Despite low genetic variation between populations, pairwise F_{ST} values indicate that population structure of round gobies at pierheads in Lake Michigan is present (Table 4). There are many possible underlying evolutionary causes that could create population structure of the round goby in Lake Michigan, such as multiple founding sources or absence of founder effects (Brown and Stepien 2009, Brown and Stepien 2008, Dillon and Stepien 2001, Dougherty et al. 1996, Stepien and Tumeo 2006, Stepien et al. 2005).

A barrier to gene flow such as long geographic distances between sites along the Lake Michigan shore could create population structure by genetic drift. As a population becomes more isolated, the potential for stochastic processes to create different genotypes in the population becomes more likely. This is known as a pattern of isolation by distance. The round goby is a small, benthic fish and its capacity to swim far distances may be limited. Adult round gobies are known to stay relatively close to their home range (Ray and Corkum 2000). A pattern of IBD was not found around the entire lakeshore (Fig. 2.a), though a significant relationship between pairwise F_{ST} and geographic distance was found on the eastern (Fig. 2.b) and on the western shores of Lake Michigan (Fig. 2.c). A pattern of IBD was not found along the northern (Fig. 2.d) or southern (Fig. 2.e) shores of Lakes Michigan. When an outlier (Muskegon and Milwaukee, distance = 633.88 km, F_{ST} = -0.015) is removed from the linear regression on the southern shore sites, a clear positive correlation between pairwise F_{ST} and geographic distance is seen (Fig. 2. f).

There are several methods of transport possible for round gobies in Lake Michigan. It has been hypothesized that the round goby was transported to the Great Lakes by uptake of larval fish in the ballast water of ships (Hensler and Jude 2007, Hayden and Miner 2008). It is likely that ships traveling through the Great Lakes move round gobies between different ports. This type of movement could breakdown isolation by distance patterns along the shore of Lake Michigan as is seen here. The Lake Ferry Express travels daily between Muskegon, MI and Milwaukee, WI for passenger transport. The pairwise F_{ST} comparison indicates that these two pierhead populations are very similar genetically ($F_{ST} = -0.015$, Table 4), while geographic distance along the lakeshore is considerable at 633.88 km. A low, non significant pairwise F_{ST} value indicates that there is probably gene flow between these two pierheads. The pairwise F_{ST} value between Ludington, MI and Manitowoc, WI is significant ($F_{ST} = 0.056$, Table 4). The SS Badger travels daily between these two ports for passenger transport. It is unclear why Ludington and Manitowoc are genetically different, while Muskegon and Milwaukee are not. Other factors not discerned may be causing these conflicting patterns of population structure, such as the depth of Lake Michigan could be a deterrent for adult round goby migration across the lake. Further information on shipping routes in the Great Lakes is needed to evaluate possible methods of round goby transport in the Great Lakes.

Lake currents are another possible mode of round goby transport in Lake Michigan. In a ten year study on climatological circulation in Lake Michigan, it was shown that the lake exhibits a stable, large scale cyclonic circulation pattern in stratified and non stratified conditions (Beletsky and Schwab 2008). Larval round gobies have been found to vertically migrate in the water column on a diel cycle (Hensler and Jude 2007, Hayden and Miner 2008). Larval yellow perch (*Perca flavescens*) were found to be transported by Lake Michigan currents (Dettmers et al. 2005), but no study has thus been done on larval round goby transport. This type of movement could potentially affect the genetic population structure of the round goby in Lake

Michigan. Further work, such as verifying if larval round gobies are actually transported by lake currents, is needed to determine if this could breakdown a pattern of IBD.

Demography, Size, and Condition

Catch per unit effort (CPUE) of round gobies caught in minnow traps was differed significantly between sites (Fig. 3). This suggests that densities vary spatially across Lake Michigan. This could be a result of different population sizes, but also an error of sampling methods. Differences in the habitat where sampling occurred, distribution of fish within a habitat, and temporal changes in density at a location could all change the CPUE even though population sizes at different locations may be similar.

 Mean weight of fish caught in minnow traps was different between sites in Lake Michigan (Fig. 4). This indicates that either environmental or genetic causes are creating a difference between fish size at different locations in Lake Michigan. Possible causes of weight difference between round gobies include environmental factors, metabolic rate, genetics, or a combination of these.

 A linear regression of the relationship between length and weight indicates the condition and health of fish. The slope of all round gobies captured by minnow traps in Lake Michigan points to fish that are in relatively healthy (Fig.5). Jude et al. (1992) found a similar relationship between length and weight of round gobies captured in the St. Claire River from 1990-1991 $(Log₁₀W = 3.4821 Log₁₀L * 5.7100, R² = 0.98)$. This relationship is very close to relationship between length and weight found by us. Round gobies in Lake Michigan have mostly the same condition between pierheads.

Conclusion

Our results show that Lake Michigan is not composed of a single, homogenous population of round gobies, but exhibits population structure in genetics, density, size, but not condition of fish. A pattern of isolation by distance explains some of the population structure we have found present in Lake Michigan. It is intriguing that there is population structure in Lake Michigan, even though it is a single body of water. Ecological and evolutionary processes may have created population structure by restriction of gene flow or by other factors. It is possible that the round goby possesses adaptive (evolutionary) potential. Further work needs be done to determine if the round goby exhibits evolutionary potential that may have facilitated its rapid establishment in the Great Lakes.

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