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NOTE

Interoceanic Sex-Biased Migration in Bluefish

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Abstract

The Bluefish *Pomatomus saltatrix* is a highly migratory species that is composed of different stocks and populations along its nearly cosmopolitan distribution. The Bluefish is the only member of its genus and family, and high migration rates could prevent vicariant speciation across its wide geographical distribution. However, the extent of gene flow between distant populations is unknown. We employed two mitochondrial genes (cytochrome-*c* oxidase subunit I and cytochrome *b*) and eight nuclear microsatellite loci to study population structure and infer dispersal of this important commercial and recreational fish across its Northern Hemisphere distribution. Higher gene flow estimates for nuclear loci (of biparental inheritance) than for mitochondrial loci (of maternal inheritance) suggested sex-biased dispersal, which could be explained by greater female homing or fidelity to spawning sites and greater dispersal of males. Males could contribute more to transoceanic connectivity of Bluefish populations in the North Atlantic Ocean, thus shaping the observed pattern of spatial genetic structure of the Bluefish in its Northern Hemisphere distribution.

Gene flow and connectivity among populations are key drivers of population dynamics and patterns of genetic structure in marine metapopulations (Cowen et al. 2000). Migration, including dispersal (emigration) and recruitment (immigration), modulates the persistence and demography of species (Hanski 1999), buffers populations against environmental fluctuations (Friedenberg 2003) or stochastic events (Cadet et al. 2003), and reduces the likelihood of local extinctions (Poethke et al. 2002). Migration patterns of marine fish can also shape patterns of population structure and may be influenced by life history strategies (Zardoya et al. 2004) and behavioral traits, such as sex-biased dispersal. Sex-biased dispersal occurs when individuals of one sex tend to be philopatric (i.e., return to the natal area to reproduce; e.g., Campos-Tellez et al. 2011) while those of the other sex tend to disperse (e.g., Cano et al. 2008). Although the term "migration" is often used to mean "movement," it has several other meanings (e.g., see Dingle 1996). Here, we use the term migration to refer to dispersal (emigration) from and recruitment (immigration) to a population.

Sex-biased dispersal is common in animals (Perrin and Mazalov 2000), including fishes. Groups such as sharks (e.g., White Shark *Carcharodon carcharias*: Pardini et al. 2001; Bonfil et al. 2005), most salmonids (e.g., Campos-Tellez et al. 2011), Weakfish *Cynoscion regalis* (Thorrold et al. 2001), and many others have been shown to exhibit differences in migratory and homing behaviors between sexes. Differences between sexes in life history traits also promote differences in dispersal. For example, if males mature later, they might migrate longer distances than females (e.g., Palo et al. 2004), as was suggested for Bluefish *Pomatomus saltatrix* (Morley et al. 2013); the opposite is probably also true. Inferences about sex-biased dispersal from observed population structuring depend on whether the examined genes are of maternal, paternal, or biparental inheritance (e.g., Prugnolle and de Meeus 2002). For example, if pairwise genetic differentiation index (F_{ST}) values (measures of genetic distance between populations) are higher for maternally inherited mitochondrial genes than for biparentally inherited nuclear DNA, this is often interpreted as an indication of higher female fidelity to particular groupings or reproductive locations (Hueter et al. 2005; Karl et al. 2011).

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Bluefish are fast-growing predators that undergo seasonal migrations related to temperature and photoperiod and also exhibit long displacements for spawning in some regions (e.g., U.S. Atlantic coast), undertaking spring or summer movements to higher latitudes, where they are often the target of recreational fisheries (Juanes et al. 1996). Bluefish reproductive behavior consists of mass spawning with external fertilization. Bluefish populations inhabit continental shelves and estuaries in temperate waters of the Atlantic, Indian, and Pacific oceans and adjacent seas (Briggs 1960; Tortonese 1986; Pottern et al. 1989; Juanes et al. 1996; Shepherd et al. 2006). In the Northern Hemisphere, Bluefish are distributed across the Atlantic Ocean and the Mediterranean Basin, including the adjacent Marmara, Aegean, and Black seas. The Bluefish is the sole member of the genus *Pomatomus* and the family Pomatomidae, and its cosmopolitan distribution (Juanes et al. 1996) indicates a high dispersal potential. However, the species seems to be spatially structured at continental and regional scales (Turan et al. 2006; Pardiñas et al. 2010). On the other hand, subtle differences in life history traits between sexes have been documented (Table 1). In general, Bluefish males mature slightly later than females; because the sex that matures later tends to migrate longer distances (Palo et al. 2004; Morley et al. 2013), we expect that male Bluefish disperse slightly farther than females. To test the hypothesis that males have a higher dispersal potential than females, we used population genetic analyses of mitochondrial DNA (mtDNA) sequences and hypervariable nuclear microsatellite loci to examine Bluefish samples spanning the Atlantic Ocean and Mediterranean Sea.

METHODS

Study area and sampling.—In total, 123 Bluefish samples were collected from eight locations across the species' northern distribution (Figure 1). Four of the sampling locations were in the northwest Atlantic Ocean along the U.S. coast: New Jersey (NJ), Maryland (MD), North Carolina (NC), and Florida (FL). One sampling location was in the northeast Atlantic Ocean: in the Bay of Cadiz (CZ) off the coast of Spain. Three sampling locations were in the Mediterranean Basin: (1) the Mediterranean Sea off the coast of Barcelona, Spain (BCN); (2) the Marmara Sea off the coast of Çanakkale, Turkey (TC); and (3) the Black Sea off the coast of Istanbul, Turkey (TI). Small pieces of muscle or fin ($\sim$1 cm^3) were dissected from each individual and were preserved in 100% ethanol prior to laboratory analyses.

Extraction, amplification, and sequencing of DNA.—Bluefish DNA was extracted with Chelex (Bio-Rad) following the method of Estoup et al. (1996). Two mitochondrial genes and eight microsatellite loci were amplified. The mitochondrial cytochrome-*b* (cyt-*b*) gene sequences were obtained with the primers H151 and L148 following the protocol and PCR conditions described by Kocher et al. (1989). The cytochrome-*c* oxidase subunit I (COI) gene was amplified with primers designed for Bluefish (COI-R-Pom: 5′-AAGAATGGGGTC-TCCTCCAC-3′; COI-F-Pom: 5′- TTGGTGCATGAGCTGG-TATG-3′) with PRIMER3 software (Rozen and Skaletsky 2000) and manually adjusted. The PCRs to obtain the COI sequences were performed using the GeneAmp PCR System2700 (Applied Biosystems, Inc. [ABI]). Total reaction volume was 40 μL, and the reaction mix contained approximately 50 ng of DNA, 20 pmol of each primer, 10 mM of Tris-HCl (pH 8.8), 250 μM of each deoxynucleotide triphosphate, 5 units of *Taq* DNA polymerase (Promega, Madison, Wisconsin), and 2.5 mM of $MgCl_2$. The PCR conditions were initial denaturing at 95°C for 5 min; 35 cycles of denaturing at 95°C for 30 s, annealing at 58°C for 30 s, and an extension at 72°C for 30 s; and a final extension at 72°C for 20 min. The PCR products were visualized in 50-mL 2% agarose gels with ethidium bromide at 10 mg/mL. Stained bands were excised from the gel, and DNA fragments were purified with an Eppendorf PerfectPrep Gel CleanUp kit. Purified DNA was precipitated using standard 2-propanol precipitation and was re-suspended in formamide prior to sequencing. Fragments were forward sequenced at the Genetic Analysis Unit, University of Oviedo, Spain, by using an ABI Prism 3100 Genetic Analyzer with the BigDye Terminator 3.1 system.

Eight tetranucleotide microsatellites—*elf17*, *elf19*, *elf37*, *elf39*, *elf44*, *elf46*, *elf49*, and *elf50* (Dos Santos et al. 2008)—

TABLE 1. Reported differences in Bluefish life history traits between sexes, as determined in three regions (Tunisia, Turkey, and the U.S. Atlantic).

Marine region	Trait	Males	Females	Reference
Tunisia	Age at maturity (years)	2.4	1.9	Dhieb et al. 2006
	Sex ratio	Monthly variation	Monthly variation	
	Size at maturity (cm)	18.1	17.1	
Turkey	Von Bertalanffy growth (cm)	48.0	51.0	Ceyhan et al. 2007
	Sex ratio		Females dominate all age-groups	
U.S. Atlantic	Age at maturity (years)	1.2	1.1	Salerno et al. 2001
	Size at maturity (cm)	33.9	33.4	
	Winter sex percentage (%)	40.4	59.6	Morley et al. 2013
	Summer sex percentage (%)	25.6	74.4	

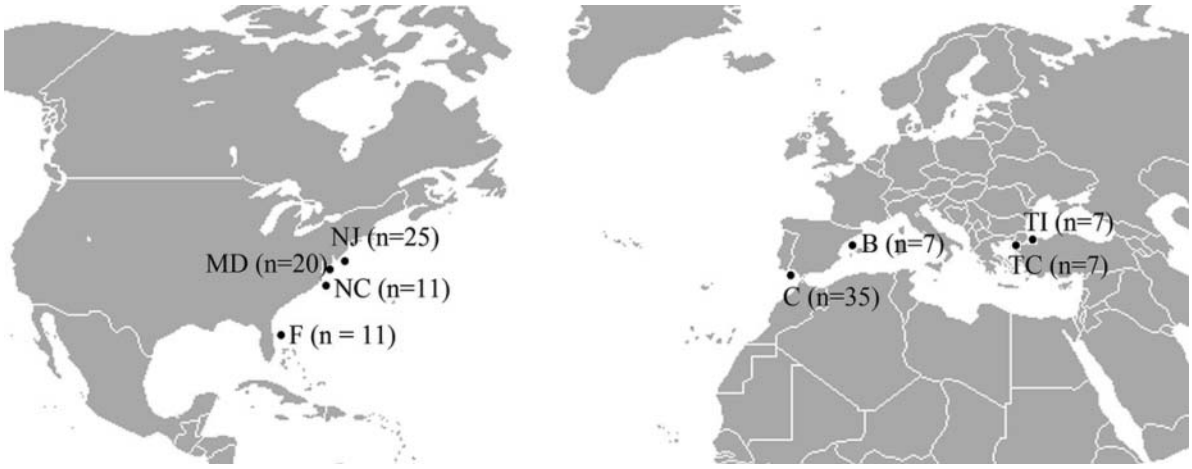

FIGURE 1. Geographical distribution of Bluefish sampling points in the Atlantic Ocean and the Mediterranean, Marmara, and Black seas (NJ = New Jersey; MD = Maryland; NC = North Carolina; F = Florida; C = Cadiz, Spain; B = Barcelona, Spain; TC = Çanakkale, Turkey; TI = Istanbul, Turkey).

were assayed with the conditions described by Dos Santos et al. (2008). Products were visualized in 2% agarose gels with 2.5 μL of ethidium bromide (10 mg/mL) to confirm amplifications and were genotyped using an ABI Prism 3100 Genetic Analyzer with a GS500 LIZ 3130 size standard at the Genetic Analysis Unit, University of Oviedo.

Genetic diversity, population differentiation, and structure.—Mitochondrial sequences were aligned using ClustalW (Thompson et al. 1994) from the BioEdit Sequence Alignment Editor (Hall 1999) for each gene. After sequence congruence was checked with the incongruence length difference test (Farris et al. 1995) implemented in PAUP* version 4.0 (Swofford 1999), the two genes were concatenated and haplotypes were defined with DNAsp version 4.50.3 (Rozas et al. 2003). Mitochondrial DNA haplotype diversity (H) and nucleotide diversity (π) were calculated for each location by using Arlequin version 3.11 (Excoffier et al. 2005).

Microsatellites were genotyped by employing GeneMapper version 4.0 (ABI). Scoring errors, large-allele dropout, and null alleles were checked with Micro-Checker (Van Oosterhout et al. 2004). Genepop (Raymond and Rousset 1995) was employed to test departures from Hardy–Weinberg equilibrium, with α adjusted using a Bonferroni correction. Microsatellite variation (number of alleles per locus, allelic richness, observed heterozygosity, and expected heterozygosity) was calculated with Genetix version 4.03 (Belkhir et al. 2001) and Fstat version 2.9.3.2 (Goudet 2001).

Genetic divergence between populations was estimated from the population pairwise values of F_{ST} obtained with Arlequin version 3.11 (Excoffier et al. 2005) using 1,023 permutations. Arlequin was also employed for Mantel tests of association, which were performed between pairwise F_{ST} values based on nuclear DNA and mtDNA to determine differences between the two genetic markers. Mantel tests were also conducted between F_{ST} values and geographical Euclidean distances to determine whether the considered populations followed an isolation-by-distance model—that is, to infer how they are structured in the study area. Minimum evolution and neighbor-joining trees based on genetic distance were performed with PHYLIP version 3.69 (Felsenstein 2005) for microsatellites and mtDNA.

Gene flow and migration rates—Migration rates between populations were calculated for mtDNA and nuclear DNA with MIGRATE version 3.0 (Beerli 2004). The program is based on coalescent theory (Beerli and Felsenstein 2001), relaxing Wright's (1951) assumptions that the population does not grow or shrink, that every individual has the same chance to reproduce, and that every generation of adults is replaced by their offspring. MIGRATE estimates $\Theta = xN_e\mu$ and $M = m/\mu$, where Θ is the mutation-scaled population size; x is the inheritance parameter ($x = 4$ for nuclear DNA [here microsatellite loci] and 1 for mtDNA); N_e is the effective population size; M is the mutation-scaled effective immigration rate; m is the immigration rate; and μ is the mutation rate. The migration estimate is often expressed as xNm, which is Θ and M multiplied together. We used this formula, employing the x for each type of data, to calculate the effective number of immigrants per generation from nuclear DNA and mtDNA. To ensure that the results would not reflect spurious local likelihood peaks, three runs were performed with the maximum likelihood method using 10 long chains (50,000 recorded steps with increments of 100) and five replicates. The MIGRATE software with the previously defined settings was run three independent times to ensure that final chains were estimating the same value of Θ for each data set (nuclear DNA and mtDNA data sets).

RESULTS

Genetic Diversity

Overall, 46 haplotypes for the concatenated COI–cyt-*b* sequences were defined in our Bluefish samples. Notably, sites

TABLE 2. Genetic variation in Bluefish at each sampling location (N = sample size; N_A = average number of microsatellite alleles per locus; A_R = allelic richness; H_e = expected heterozygosity; H_o = observed heterozygosity; N_h = number of mitochondrial haplotypes; H = haplotype diversity; π = nucleotide diversity).

Locality	Acronym	N	N_A	A_R	H_e	H_o	N_h	H	π
New Jersey	NJ	25	14.1	13.19	0.8853	0.7021	14	0.9264 ± 0.0388	0.0045 ± 0.0026
Maryland	MD	20	13.1	12.52	0.8714	0.7576	16	0.9692 ± 0.0209	0.0051 ± 0.0029
North Carolina	NC	11	16.4	7.96	0.8399	0.7549	8	0.9273 ± 0.0665	0.0051 ± 0.0030
Florida	FL	11	10.1	9.09	0.8593	0.6598	9	0.9636 ± 0.0510	0.0056 ± 0.0033
Cadiz, Spain	CZ	35	14.6	13.68	0.8014	0.7170	11	0.8414 ± 0.0441	0.0025 ± 0.0016
Barcelona, Spain	BCN	6	6.7	6.02	0.7143	0.7619	6	1.0000 ± 0.0962	0.0031 ± 0.0021
Çanakkale, Turkey	TC	7	6.7	4.09	0.7194	0.8299	1	0.0000 ± 0.0000	0.0000 ± 0.0000
Istanbul, Turkey	TI	7	6.0	4.08	0.7211	0.6922	3	0.5238 ± 0.2086	0.0006 ± 0.0006
Total		122	23.28	20.75	0.839	0.741	46	0.9344 ± 0.0140	0.0086 ± 0.0023

in the western Atlantic exhibited more haplotypes and higher H and π values than eastern Atlantic sites. The number of haplotypes per site varied from 1 in the TC samples to 16 in the MD samples. The concatenated fragments were 881 bp long and were composed of 570 bp from the COI gene plus 311 bp from the cyt-*b* gene (GenBank accession numbers JQ039400–JQ039435 for COI; JQ039436–JQ039465 for cyt-*b*). Fragments had 10 variable sites that differentiated the two sides of the Atlantic Ocean and another 39 variable positions that defined all described haplotypes. We generally found high H and low π in all regions (Table 2).

Micro-Checker did not detect dropouts or scoring errors in the eight microsatellite loci considered, but null alleles were found for *elf44* in different sampling locations, so this locus was excluded from analyses. Samples were in Hardy–Weinberg equilibrium and exhibited similar levels of variation as measured by allelic richness and heterozygosity (Table 2), despite the fact that BCN, TC, and TI sample sizes were smaller than the rest; this suggests that the study is adequate and that our results are robust.

Population Differentiation and Population Structure

Pairwise F_{ST} comparisons revealed three different genetic clusters—American (NJ, NC, MD, and FL), Spanish (BCN and CZ), and Turkish (TI and TC)—for both mitochondrial and nuclear markers (Table 3). However, we did detect differences between the two markers, as mitochondrial F_{ST} values were

TABLE 3. Pairwise estimates of the genetic differentiation index (F_{ST}; below the diagonal) between Bluefish samples based on mitochondrial DNA or microsatellite loci. Associated P-values are given above the diagonal; significant P-values are in bold italics. Sampling locality acronyms are defined in Table 2.

Locality	NJ	MD	NC	FL	CZ	BCN	TC	TI
Mitochondrial DNA								
NJ		0.18919	0.15315	0.07207	***0.00000***	***0.00000***	***0.00000***	***0.00000***
MD	0.02436		0.71171	0.62162	***0.00000***	***0.00000***	***0.00000***	***0.00000***
NC	0.04170	−0.02772		0.90090	***0.00000***	***0.00000***	***0.00000***	***0.00000***
FL	0.05955	−0.02595	−0.05941		***0.00000***	***0.00000***	***0.00000***	***0.00000***
CZ	***0.75687***	***0.74427***	***0.75280***	***0.74692***		0.91892	***0.01892***	***0.00000***
BCN	***0.70537***	***0.68326***	***0.67787***	***0.65902***	−0.06545		***0.00000***	***0.00000***
TC	***0.74745***	***0.73286***	***0.74596***	***0.73079***	***0.19134***	***0.18157***		0.99099
TI	***0.75434***	***0.74041***	***0.75938***	***0.74326***	***0.23288***	***0.17656***	0.00001	
Nuclear microsatellite loci								
NJ		0.15137	0.57324	0.50684	***0.00000***	***0.00977***	***0.00000***	***0.00000***
MD	0.01008		0.25391	0.67285	***0.00195***	***0.03809***	***0.00000***	***0.00000***
NC	0.00367	0.01153		0.20312	***0.01855***	0.09473	***0.00098***	***0.00391***
FL	0.00498	0.00240	0.01777		0.05469	***0.00781***	***0.00391***	***0.02734***
CZ	***0.02203***	***0.01930***	***0.01969***	0.01357		0.41699	***0.00098***	***0.00195***
BCN	***0.03900***	***0.03542***	0.02785	***0.04297***	0.00572		***0.00000***	***0.00293***
TC	***0.06407***	***0.08319***	***0.07205***	***0.06358***	***0.07385***	***0.05565***		0.12891
TI	***0.06734***	***0.07287***	***0.06623***	***0.04482***	***0.07825***	***0.04119***	0.01869	

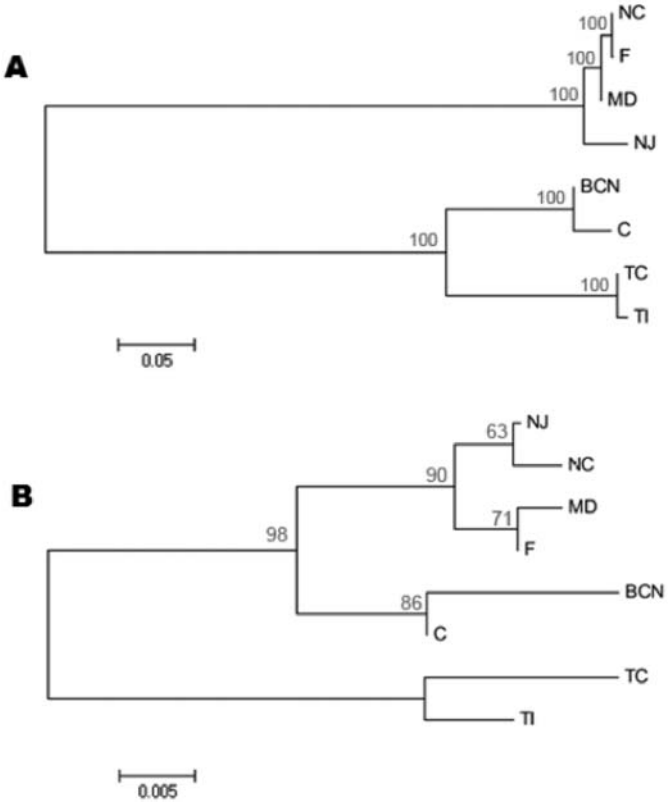

FIGURE 2. Neighbor-joining trees based on genetic differentiation index (F_{ST}) values calculated from Bluefish **(A)** mitochondrial DNA and **(B)** nuclear microsatellite loci. Sampling locality acronyms are defined in Figure 1.

always higher than nuclear F_{ST} values. Two combinations of samples from Spain and the USA were not significantly different: CZ versus FL ($P = 0.05469$) and BCN versus NC ($P = 0.09473$). The differences between genetic markers were also reflected in the neighbor-joining trees that were constructed based on genetic distances (Figure 2). The position of the branch containing the Spanish samples (CZ [eastern Atlantic] and BCN [western Mediterranean Sea]) varied in the trees built from the different markers, clustering with the eastern Mediterranean clade for mtDNA and with the American clade for microsatellites (Figure 2). The minimum evolution trees (data not shown) were identical to the neighbor-joining trees.

Mantel tests revealed a low correlation between mitochondrial and nuclear genetic markers ($r = 0.496$, $P = 0.02$) suggesting a low but correlated pattern in genetic distances from maternally inherited (mtDNA) and biparentally inherited (nuclear) markers. Furthermore, a high and significant correlation was detected between genetic distances and Euclidean distances between samples ($r = 0.734$, $P < 0.001$), implying a pattern of isolation by distance for Bluefish.

Gene Flow and Migration

To estimate gene flow and improve the analysis by avoiding small sample sizes, the samples were clustered into the three main geographical units defined above. As expected from the previously described results, estimates of gene flow (mean effective number of immigrants per generation and for each genetic unit) were significantly different for mtDNA and microsatellites (Figure 3) in all cases (paired t-test: $P \leq 0.05$), using the corresponding inheritance parameters (x) in the calculations to make the different markers comparable. Effective number of immigrants, mean Θ values, and their 95% confidence intervals are shown in Figure 3. We observed asymmetrical gene flow among regions for the two marker types. Values ranged from 0.02 to 1.62 immigrants/generation for mtDNA and from 0.98 to 3.49 immigrants/generation for microsatellite loci. For the Mediterranean Sea samples, the asymmetry was in opposite directions for the two markers: more intense westward migration was indicated by microsatellite loci, and eastward migration was indicated by mtDNA. For samples from the Atlantic Ocean, asymmetry between markers was not detected. In both cases, the estimated gene flow was more intense from the USA to Spain. The main difference between markers in the Atlantic Ocean samples was that the total number of immigrants (detected with microsatellite loci) from Spain to the USA was 91 times stronger than the number of female immigrants (detected with mtDNA). Unexpectedly, for both markers, estimates of gene flow across the Atlantic Ocean were similar in magnitude to estimates of gene flow across the Mediterranean Sea, despite the large difference in geographical scale.

DISCUSSION

Based on indirect evidence from genetic analyses, the results of this study suggest the occurrence of transoceanic effective migration for Bluefish across the Atlantic Ocean. Transoceanic passage would be possible for this species given its migratory lifestyle, as has been shown for other species such as sharks (Bonfil et al. 2005) and tunas (Block et al. 2001). Larval transport in the Gulf Stream (as suggested by Hare and Cowen 1993) does not seem sufficient to account for the transoceanic differences we have documented here, given that (1) Bluefish larvae complete their development near the surface and (2) juveniles are generally found on continental shelves, bays, estuaries, and shallow waters (Kendal and Walford 1979; Juanes et al. 1996). Instead, active migration by adult Bluefish is a more likely explanation. Bluefish migration may be temperature dependent (see Goodbred and Graves 1996), and glacial periods have been identified as isolation stages for this species (Pardiñas et al. 2010); therefore, current interglacial conditions may be promoting Bluefish dispersal. Pairwise F_{ST} values (measures of genetic distance between populations) based on mtDNA were all higher than those based on nuclear DNA. Higher pairwise F_{ST} values for maternally inherited mitochondrial genes than for biparentally inherited nuclear DNA are often interpreted as indicating higher female fidelity to particular groupings or reproductive

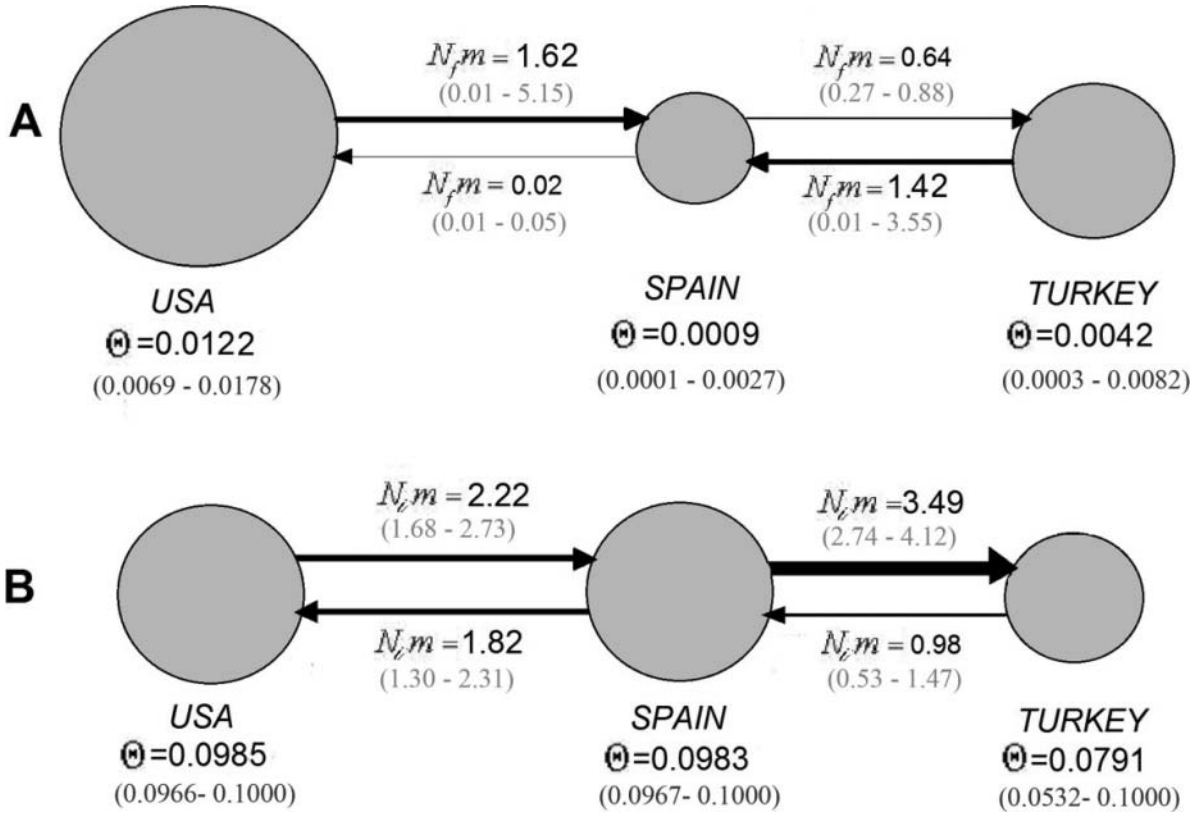

FIGURE 3. Gene flow across the detected Bluefish genetic units. Gray circles represent population units and are proportional to theta (Θ; the mutation-scaled population size) values. Gene flow as number of migrants per generation (*Nm*) is represented with arrows (95% confidence intervals are shown in parentheses below the mean values): **(A)** number of female migrants per generation ($N_f m$) based on mitochondrial DNA; and **(B)** number of migrants per generation ($N_f m$) based on nuclear microsatellite loci.

locations (Hueter et al. 2005; Karl et al. 2011). Moreover, much lower estimates of gene flow were obtained for mtDNA than for microsatellites, suggesting some homing fidelity in females (lower migration rates) but not males (Hueter et al. 2005). Both results suggest that Bluefish females have genetic barriers to dispersal. Further support for sex-specific migration comes from a recent study using the scales of adult Bluefish collected in NC, where males disproportionately (relative to females) migrated out of the South Atlantic Bight in the summer (Morley et al. 2013). Other highly migratory fish species, including salmonids, seem to exhibit sex-biased dispersal (Campos-Telles et al. 2011), but this is the first time that homing fidelity and sex-biased dispersal have been suggested for Bluefish.

Understanding the dynamics of sex-specific movements has both ecological and evolutionary implications. Although Bluefish do not exhibit sexual dimorphism (Pottern et al. 1989), small differences in life history traits between males and females have been reported (Table 1). From these differences and based on the hypothesis that maturity influences migration strategy (Palo et al. 2004; Morley et al. 2013), we expected that male Bluefish would be able to disperse slightly farther than females because males mature later and at larger sizes (Salerno et al. 2001; Dhieb et al. 2006), thus affording greater swimming ability. The results of this study not only support our expectation but also suggest that slight differences in life history traits can have important consequences for population structuring. Behavior, together with life history differences, can explain the differing migration estimates for maternally and biparentally inherited markers in this species. Such differences could also lead to sex-specific selective constraints, such as higher dispersal costs or lower postmigratory breeding success for females (Cano et al. 2008). Unfortunately, little work has focused on adult Bluefish behavior; our results suggest that additional work on this subject is greatly needed.

In addition to trans-Atlantic migration, trans-Mediterranean migration apparently also occurs in Bluefish. Highly asymmetric gene flow, which was more intense from west to east when estimated from microsatellites and vice versa when estimated from mtDNA (Figure 3), again suggests differences in dispersal behavior between males and females. Differences in the asymmetric pattern found in the Mediterranean Sea relative to the Atlantic Ocean could be due to the N_e (proportional to Θ values, which are represented in Figure 3 with different circle sizes). In other words, the genetic units with higher N_e may provide more migrants to the smaller populations. For

example, based on our mtDNA results, more migrants go to Spain (with the lowest Θ value) from both the USA and Turkey because these latter populations have larger values of N_e. The general trend was similar in the case of nuclear DNA. Differences in the relative level of asymmetry between the two markers as seen across the Mediterranean Sea, where the asymmetry is more marked, could also be due to differences in N_e. Physical tag–recapture experiments (of the sort summarized by Shepherd et al. 2006, but including sex-specific information) would confirm these results based on population genetic methodology.

In conclusion, our results depict patterns of genetic population structure of Bluefish in the species' northern distribution, consistent with sex-biased dispersal and transoceanic migration. Different patterns between the two genetic markers, including lower migration rates and stronger genetic barriers inferred from mtDNA (maternally inherited) relative to those inferred from microsatellite loci (biparentally inherited), suggest male-mediated gene flow among regions and greater philopatry in females. Trans-Atlantic migratory movements and subsequent gene flow could explain the lack of divergence in Bluefish populations, thereby maintaining a single species across the Atlantic Ocean and in the family Pomatomidae.

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