A Tale of Two Skates: Comparative Phylogeography of North American Skate Species with Implications for Conservation

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Genomic data can provide novel insights into the natural history of oceanic species. These data can inform the management of vulnerable and slow-maturing species by estimating population structure, rates of migration, and the distribution of genetic diversity. In this study we focus on two protected elasmobranch species, the Winter Skate, *Leucoraja ocellata,* and the Little Skate, *L. erinacea*. We use genome-wide SNPs to estimate population structure, and quantify migration and genetic diversity among both species from four sampling localities across the Atlantic coast of North America. We find that species of *Leucoraja* are generally isolated by distance, although we infer some fine-scale population structure. Specifically, estimates of effective migration infer fine-scale population structure in *L. ocellata* between the northern sites of Georges Bank and the Mid-Atlantic sampling sites, whereas *L. erinacea* shows no evidence of population genetic structure in any analyses. We also found that genetic diversity is concentrated in the central sites of Georges Bank and the Mid-Atlantic Bight for *L. ocellata,* but is reduced at these two sites in *L. erinacea,* suggesting opposite distributions of genetic diversity between species. Thus, genomic data suggest that while species of *Leucoraja* lack discrete population structure, they likely employ only mid-range dispersal. These findings correspond to ecological studies that have found eco-physiological differences between embryonic and juvenile *Leucoraja* from different localities. Taken together, small-bodied skate research emphasizes the importance of local adaptive plasticity for marine species, even without population genetic structure. Conservation strategies should focus on managing the portions of the Atlantic coast considered most vital to reproduction of *Leucoraja,* but should not recognize multiple populations across their range.

UNDERSTANDING the population structure and movement patterns of marine species is fundamental for effective management and conservation strategies. This is especially important when multiple stressors at both local and global scales are impacting species (Benestan et al., 2016; Stockwell et al., 2016). In fact, many marine animals are experiencing physical and chemical changes in their environment at a rate they may never have experienced in their evolutionary history (Pörtner et al., 2014). Nonetheless, species that possess intraspecific variability across populations, potentially driven by adaptation to local environmental conditions, may be more resilient to directional changes in the environment (Di Santo, 2016). One of the most effective ways to measure such intraspecific variation is to analyze population structure, quantify gene flow, and estimate centers of genetic diversity across the geographic range of a species (Hauser and Seeb, 2008). Yet, population genetic variation is challenging to estimate in oceanic species, which often demonstrate subtle population structure in the absence of geographical barriers (Griffiths et al., 2010; Portnoy and Heist, 2012; Boehm et al., 2015).

Batoids (skates and rays) are a large group of mostly benthic elasmobranch fishes, characterized by slow development and maturity, and low fecundity when compared to bony fishes (Frisk, 2004). Many benthic species within this group exhibit high philopatry and high costs of locomotion (Di Santo and Kenaley, 2016; Di Santo et al., 2017), which limit long-distance movements (Musick et al., 2004; Wearmouth and Sims, 2009). This may therefore inhibit their ability to recolonize areas following local population extirpation (Dulvy and Reynolds, 2002; Di Santo and Kenaley, 2016; Di Santo et al., 2017). As such, skates are particularly vulnerable to overexploitation and changes in the environment due to their life history characteristics and behaviors (Stevens et al., 2000; Dulvy and Reynolds, 2002; Frisk and Miller, 2006; Di Santo et al., 2016). Oviparous elasmobranchs may also be more sensitive to habitat alteration because they require suitable spawning habitat for the embryos, which develop slowly inside the egg case and cannot thermoregulate (Frisk, 2010; Di Santo, 2015).

This study focuses on two benthic oviparous elasmobranch species, the Winter Skate *Leucoraja ocellata*, and the Little Skate *L. erinacea*. Both species are co-distributed along the Atlantic coast of North America (Fig. 1; Frisk et al., 2002; Alvarado et al., 2005; Frisk and Miller, 2006). *Leucoraja ocellata* is distributed from Labrador, Canada, to Cape Hatteras, USA. This species exhibits a narrow latitudinal range, has declined substantially in Canadian (up to 98% in certain regions) and U.S. (~50% since the 1970s) waters, and is considered endangered by the IUCN (McPhie, 2007; IUCN, 2016). Life history of *L. ocellata* has been studied from five localities (from north to south): southern Gulf of St. Lawrence; Scotian Shelf; Southern Gulf of Maine (GM)/ Georges Bank (GB); Mid-Atlantic Bight (MA); and Cape Hatteras (CH; Frisk et al., 2002; Frisk and Miller, 2006, 2009).

Leucoraja erinacea is sympatric with *L. ocellata*, but its range does not extend as far north (Frisk and Miller, 2006). *Leucoraja erinacea* is most abundant in GB and MA, which

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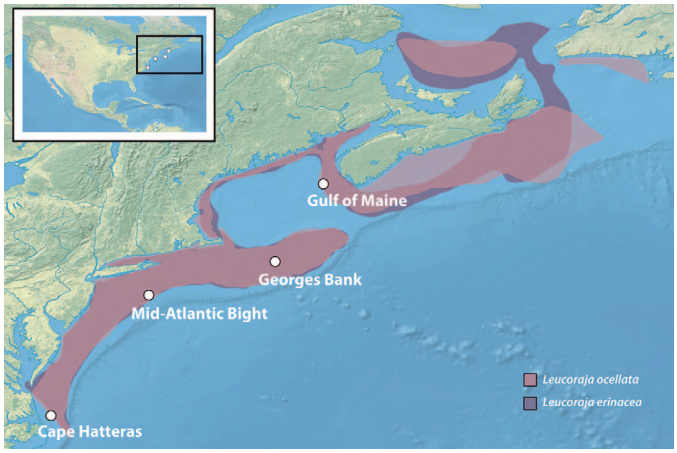

Fig. 1. Range map of distributions of *Leucoraja ocellata* (pink) and *L. erinacea* (purple) in eastern North America. The four sampling localities used in this study are shown with white circles. Species ranges were redrawn from IUCN (2016) range maps.

also represents the center of their distribution (Frisk and Miller, 2006). This species is considered near threatened by the IUCN due to harvest as bycatch and for use as lobster bait (IUCN, 2016). Likewise, this species is thought to exhibit limited dispersal capabilities due to high metabolic rates during swimming, thus putatively favoring the evolution of locally adapted populations (Frisk et al., 2008; Di Santo, 2016; Di Santo and Kenaley, 2016).

These two skate species exhibit a number of differences in both body size and rate to adult maturity. *Leucoraja erinacea* mean body size is inversely related to temperature, with larger individuals found at higher latitudes and smaller individuals at lower latitudes, whereas *L. ocellata* exhibits smaller body sizes at higher latitudes (McEachran and Martin, 1977; McPhie, 2007). In addition, empirical data have demonstrated that embryos and juveniles of *L. erinacea* in two adjacent localities (GM and GB) exhibit significant metabolic and performance differences even when developmentally acclimated in common garden conditions (Richards et al., 1963; Di Santo, 2015, 2016). Similarly, other skate species have shown evidence of local adaptation (Templeman, 1987; Ebert et al., 2008). Taken together, latitudinal gradients in body size and local eco-physiological adaptation support the possibility of population genetic structure, despite lacking discrete barriers to gene flow (Frisk, 2004). Alternatively, these local adaptive responses could be driven by epigenetic changes, and therefore may be decoupled from wider population genetic structure (Lighten et al., 2016). Building on past investigations of the ecology of *Leucoraja*, this study investigates several questions: (1) Do *Leucoraja ocellata* and *L. erinacea* demonstrate discrete population genetic structure? (2) Do patterns of gene flow between putative populations suggest long-range or local movement patterns? (3) How is genetic diversity partitioned in both species, and how should this inform management practices? (4) Do *Leucoraja ocellata* and *L. erinacea* consist of multiple management units?

MATERIALS AND METHODS

Sampling and SNP data generation.—We extracted DNA from fin clips using a standard phenol-chloroform extraction protocol. Our sampling consisted of 55 *L. ocellata* collected from the Gulf of Maine (GM; $n = 10$), Georges Bank (GB; $n = 20$), Mid-Atlantic (MA; $n = 20$), Cape Hatteras (CH; $n = 5$; Fig. 1). Moreover, we sampled 72 *L. erinacea* from GM ($n = 16$), GB ($n = 20$), MA ($n = 20$), and CH ($n = 16$). We prepared double-digest restriction site associated DNA sequencing (ddRADseq) libraries following Peterson et al. (2012). Briefly, we digested 500 ng of DNA per individual using 20 units of *Sbf*I and 20 units of *Msp*I (NEB) for eight hours at 37°C in 1X CutSmart Buffer (NEB). We ligated barcoded Illumina TruSeq adapters at 16°C for 23 minutes and heat killed the enzyme at 65°C for 10 minutes. Each adapter included an eight-base-pair (bp) unique molecular identifier that helped to increase the diversity of colonies on the flow cell (Streicher et al., 2014). We pooled 12–13 uniquely barcoded individuals into each group and labeled each with a TruSeq single index. We size selected all groups using the Blue Pippin electrophoresis platform (Sage Science, Beverly, MA) for fragments between 435–535 bp. Libraries were amplified using indexed Illumina® paired end PCR primers with Phusion® High Fidelity Proofreading Taq (NEB) under the following thermocyler conditions: initial denaturation at 98°C for 30 sec, 15 cycles of 98°C for 30 sec, 55°C for 30 sec, 72°C for 1 min, and a final extension at 72°C for 5 min. We confirmed successful library preparation using a 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA) with a DNA 7500 chip kit. Final concentrations were verified using a Qubit®. We pooled our 11 sub-libraries in equimolar amounts and sequenced our final library (100 bp fragments, paired end run) on a single lane of the Illumina® HiSeq 2500 at the Brigham Young University DNA Sequencing Center (https://dnasc.byu.edu).

We processed our raw sequence data using the Stacks v. 1.35 pipeline (Catchen et al., 2011). We began with process_radtags with both forward and reverse reads, which filtered out reads below 90% quality score threshold. We used Bowtie2 v. 3.21 (Langmead and Salzberg, 2012) under default parameters to map merged reads to the genome of *L. erinacea* downloaded from Ensembl (Wang et al., 2012). We then followed the standard Stacks workflow beginning with (i) pstacks, which filtered out loci with less than 3x read depth, (ii) cstacks, which creates a catalogue of all of loci among all individuals (–n flag, setting of 0), (iii) sstacks, which searches the stacks created in pstacks against the catalogue from cstacks, and (iv) populations, which genotypes each individual according to the matched loci from sstacks. We ran populations with an –r flag = 0.7 in *L. ocellata* and –r = 0.8 in *L. erinacea*, thus requiring each SNP to be present in at least 70% and 80% of individual samples, respectively (all individuals assigned to one population during filtering). We further filtered our data with custom python scripts to remove loci with more than two SNPs, remove invariant loci, and remove individuals with more than 40% missing data (Portik et al., 2017; https://github.com/dportik/Stacks_pipeline). We used these filtered data to create input files for downstream analyses. We first ran the Stacks pipeline on all individuals of both species together, and used Structure v. 2.3.4 (Pritchard et al., 2000) to identify 11 samples misclassified at the species level (results not shown). After removing these 11 samples, we ran the Stacks pipeline separately for both species to increase the number of shared loci and minimized missing data caused by allelic dropout (Arnold et al., 2013). After all filtering steps, we retained 31 individuals with 524 SNPs for *L. ocellata* ($n = 3$ Gulf of Maine, $n = 10$ Georges Bank, $n = 16$ Mid-Atlantic, $n = 2$ Cape Hatteras) and 57 individuals with 452 SNPs for *L. erinacea* ($n = 10$ Gulf of Maine, $n = 17$ Georges Bank, $n = 19$ Mid-Atlantic, $n = 12$ Cape Hatteras). Final fastq files can be accessed from the

NCBI Short Read Archive numbers SAMN08994975–SAMN08995088.

Investigating population structure.—We implemented a series of analyses to test if species of *Leucoraja* demonstrated discrete population genetic structure. First, we estimated pairwise FST using the package 'Adegenet.' v. 2.1.1 using the *pairwise.FST* function (Jombart, 2008) in *R* (R Core Team, 2017). We tested if *Leucoraja* were isolated by distance at the individual using a Mantel test in 'Adegenet.', testing 99,999 permutations. We compared Euclidean genetic distances of individuals with Euclidean geographic distances of sampling localities.

We further explored population structure using both model-free and model-based clustering analyses. First we implemented principal component analyses (PCA) using the *dudi.pca* function implemented in 'Ade4' (Dray and Dufour, 2007). We retained the first 25 PCs. We further estimated population structure using maximum likelihood in ADMIXTURE v. 1.3.0 (Alexander et al., 2009) using a range of *K* values (1–10), with five iterations per *K* value. Finally, we explored population structure using the program fineRADstructure v. 0.3 (Malinsky et al., 2018). fineRADstructure utilizes the information from multiple SNPs per locus to calculate the co-ancestry matrix, a summary of nearest-neighbor haplotype relationships. Individuals were assigned to populations using finestructure with 100,000 burn-in generations, 100,000 MCMC iterations, and with a thinning interval of 1,000. We performed tree building (simple cladogram) using 10,000 burn-in generations and visualized the resulting co-ancestry plot using FineSTRUCTURE GUI v. 0.0.2 (Lawson et al., 2012).

Estimating genetic diversity and levels of gene flow.—We estimated global and population level expected heterozygosity (H_e) using 'Adegenet.' Further, we visualized the spatial distribution of genetic diversity and patterns of effective migration in each species using the program EEMS (Petkova et al., 2015). EEMS identifies geographic regions where genetic dissimilarity decays more quickly than expected under a null model of isolation by distance. It relates effective migration rates to expected genetic dissimilarities to identify regions of high or low migration. The program also estimates levels of effective genetic diversity across the landscape on the basis of genetic distances between individuals sampled within a given site (deme). As such, localities with more dissimilar individuals are estimated as regions of higher genetic diversity. This estimate of diversity is expected to correlate with heterozygosity (Petkova et al., 2015). Three independent chains were run for each species, using a deme size of 500 for 8,000,000 MCMC iterations, with 3,200,000 iterations of burn-in and 9,999 thinning iterations. We checked convergence and visualized effective migration and diversity surfaces using the accompanying plotting program 'rEEMSplots' in RSTUDIO v. 3.4.3 (Racine, 2012; Petkova et al., 2015).

RESULTS

Species of Leucoraja exhibit weak population structure.—Population genetic analyses were generally unable to identify population structure within either species. We inferred values of FST between sampling localities in both species ranging from 0.0–0.12. Although overall FST was higher in *L. erinacea* (0.06) than in *L. ocellata* (0.04), we found no significant difference between the FST values between species (Table 1). We inferred different patterns between species in the Mantel tests (Fig. 2A–D). Whereas the analysis rejected IBD for *L. ocellata* ($P = 0.10$; observed value = –0.21; Fig. 2C), it supported IBD in *L. erinacea* ($P = 0.003$; observed value = 0.16; Fig. 3D). The cross-validation approach from maximum likelihood clustering supported $K = 1$ for both species (Fig. S1A–B; see Data Accessibility), and the principal component analyses also failed to identify clusters corresponding to geographic sampling locations (Fig. S1C–D; see Data Accessibility). Finally, fineRADstructure did not differentiate individuals between sampling sites in the pairwise co-ancestry matrix (Fig. 3A–B). This is noted by a lack of similar-colored (more genetically similar) clusters on the diagonal, rather than scattered colors as we observed.

Table 1. FST estimates for *Leucoraja ocellata* (bottom) and *L. erinacea* (top) inferred from SNP data from four sites across their geographic range. Sampling sites are abbreviated as follows: GM = Gulf of Maine, GB = Georges Bank, MA = Mid-Atlantic, CH = Cape Hatteras.

	GM	GB	MA	CH
GM	—	0.07	0.06	0.08
GB	0.12	—	0.05	0.06
MA	0.08	0.05	—	0.05
CH	0	0	0	—

Patterns of gene flow and measures of genetic diversity differ between sites.—Expected heterozygosity (H_e) was significantly different between species (t-test, $P = 0.01$; Table 2). Mean expected heterozygosity was higher in *L. ocellata* than in *L. erinacea* (0.139 vs. 0.077). Within *L. ocellata*, expected heterozygosity ranged from 0.059–0.153. Expected heterozygosity was highest in the south (CH) and lowest in the north (GM), though this diversity pattern may have been influenced by the reduced number of samples from GM and CH (Table 2). In *L. erinacea,* H_e ranged from 0.067–0.073 and was highest in the south (CH). Diversity was relatively even between populations in *L. erinacea*, though it was lower in the two central localities (GB and MA) than in the north and south (GM and CH; Table 2).

Estimates of effective migration surfaces for *L. ocellata* inferred higher levels of effective migration than expected under a model of IBD between CH and MA, but reduced migration between GB and GM (Fig. 4A). In *L. erinacea*, EEMS estimated a pattern of strict IBD, and inferred no migration between sites above the null level (of IBD; Fig. 4B). Estimates of effective diversity surfaces for *L. ocellata* inferred elevated diversity in the central localities of MA and GB, but reduced genetic diversity in northern and southern localities (Fig. 4C). This differed from estimates of expected heterozygosity that suggested that the highest genetic diversity occurred in the south at CH. However, this discrepancy may be a sampling artifact as we had few samples of *L. ocellata* from the north and south after SNP filtering. Estimates of genetic diversity for *L. erinacea* suggested lower than expected diversity in the two central localities (corresponding to slightly lower H_e) but did not identify any one locality with elevated levels of genetic diversity (Fig. 4D). This corresponded to the relatively even levels of H_e between sites and suggests that genomic variation is evenly partitioned across sites in this species.

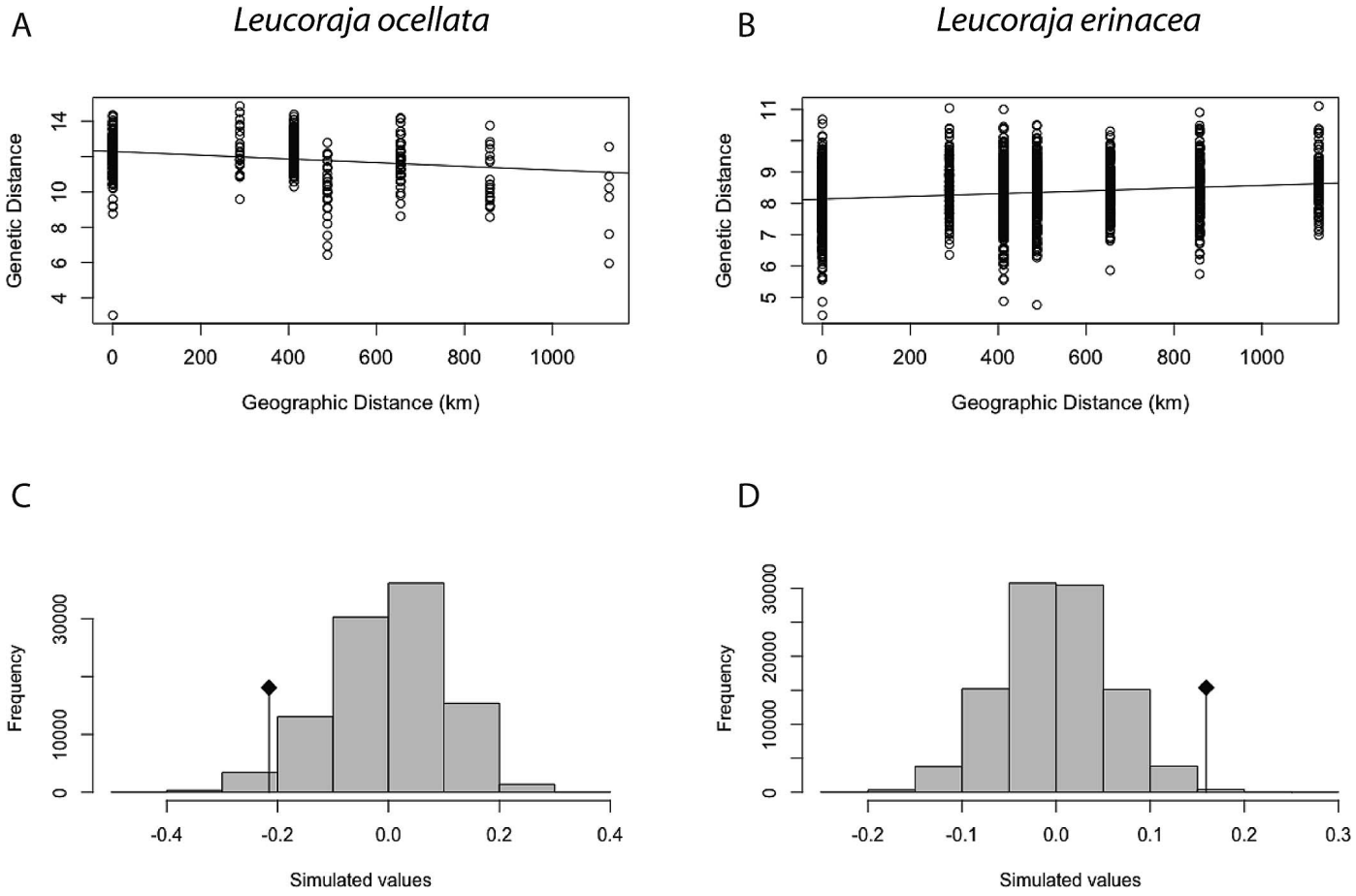

Fig. 2. Tests of isolation by distance patterns in *Leucoraja ocellata* and *L. erinacea*. (A–B) Scatter plot of genetic distance against geographic distance suggesting a negative relationship between distances for *L. ocellata*, but a positive relationship in *L. erinacea*. (C–D) Mantel test results support a significant isolation by distance pattern for *L. erinacea*, but not for *L. ocellata*.

DISCUSSION

The distribution of genetic variation in adult individuals of *L. ocellata* and *L. erinacea* is primarily determined by geographic distance along the Atlantic coast of North America. In *L. erinacea*, we recovered a strict pattern of IBD in multiple analyses, suggesting that discrete barriers do not limit movements in this species. Alternatively, the Mantel test and EEMS failed to support IBD in *L. ocellata*. This suggests the potential for fine-scale genetic structure in this species, though fineRADstructure did not infer any geographic structure. Thus, inferences of structure may be artifacts of reduced sample sizes in the northern and southern populations, rather than indications of barriers to dispersal.

Patterns of genetic diversity differed between species, with higher diversity in central localities in *L. ocellata* and reduced genetic diversity in central localities in *L. erinacea*. In addition, *L. ocellata* exhibited elevated levels of gene flow between southern localities, compared with a pattern of strict IBD in *L. erinacea*. These results complement recent ecological studies that suggest that many small-bodied skates have a low capacity for dispersal and that females are highly philopatric (Perry et al., 2005; Lauder and Di Santo, 2015; Di Santo et al., 2017). As such, conservation and management practices should focus on the critical habitat (perhaps spawning habitat) because local populations do not move long distances (Hoff, 2010). The two skate species in this study exhibited different patterns of genetic diversity (Table 2; Fig. 4C–D). First, we inferred higher levels of genetic diversity in *L. ocellata* than in *L. erinacea* (Table 2). Second, we identified variation in the level of genetic diversity between populations in *L. ocellata*. Expected heterozygosity was highest in central and southern localities, while EEMS recovered the highest level of genetic diversity in the two central localities. We inferred no significant differences in genetic diversity between populations of *L. erinacea*. Nonetheless, this discrepancy may be due to our sampling regime. We had fewer samples in *L. ocellata* from GM and CH, the two localities EEMS inferred to have low diversity. With equal sampling, the distribution of genetic diversity may have been more equal in *L. ocellata* as observed in *L. erinacea*. Future studies should aim to sample both species more widely, and sample more individuals per locality. More equal sampling may confirm if we recovered a biologically 'real' pattern of genetic diversity in *L. ocellata*.

Past ecological studies have found that species of *Leucoraja* prefe short-distance movement strategies due to physical constraints driven by oxygen consumption (Lauder and Di Santo, 2015; Di Santo and Kenaley, 2016; Di Santo et al., 2017). In addition, female skates are generally thought to exhibit breeding site philopatry (Vargas-Caro et al., 2017). These life history characteristics lend themselves well to a pattern of IBD in *L. erinacea* and population structure in central localities in *L. ocellata*, suggesting that species of *Leucoraja* do not regularly undertake long-distance movement, but that enough gene flow does occur over short distances to prevent local genetic differentiation between

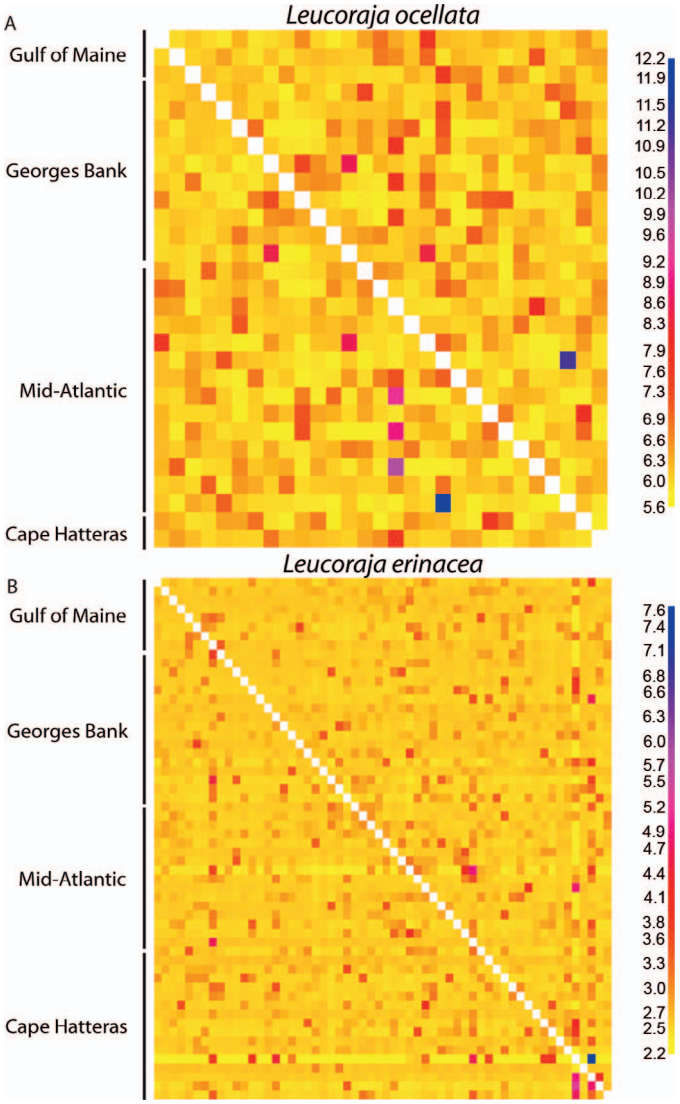

Fig. 3. Pairwise coancestry matrix for *Leucoraja ocellata* (A) and *L. erinacea* (B). Sampling localities are labeled on the y-axis. If the program had recovered discernable population structure, clusters of similar colors would appear along the diagonal. However, a lack of visible clusters of genetically similar individuals supports the absence of discrete population structure in both species.

most localities. Similarly, EEMS uncovered higher rates of gene flow than expected under IBD between southern localities of *L. ocellata*. This increased gene flow may suggest that southern individuals of *L. ocellata* are capable of dispersing longer distances than northern individuals, perhaps due to their larger body sizes (McPhie, 2007). The highest FST measure in *L. ocellata* was inferred between the two northern populations, GM and GB, further supporting decreased movement by northern individuals (which were more differentiated). Large-bodied skates have been known to disperse very long distances (>2000 km; King and McFarlane, 2010; Farrugia et al., 2016), but in small-bodied species much shorter average movement distances are common (Wearmouth and Sims, 2009). Additionally, species that exhibit population structure do so over much larger distances than we investigated in this study (Reiss et al., 2009). Several past studies have found evidence for local adaptation in one of these skate species (Frisk, 2004; Frisk and Miller, 2006, 2009; Di Santo et al., 2016; Lighten et al., 2016). Local adaptation, despite a lack of population genetic structure, suggests that ecological plasticity plays an important role in the persistence of marine species, especially in the face of future climate change (Di Santo and Lobel, 2016, 2017). This propensity for local adaptation (even in the face of rapid climate changes) is surprising given slow maturation and low fecundity of skates (Lighten et al., 2016).

Table 2. Sampling localities, sample sizes (after filtering), and estimated heterozygosity (H_e) for *Leucoraja ocellata* and *L. erinacea*.

Population	*n*	Latitude	Longitude	H_e
Leucoraja ocellata				
Gulf of Maine	3	43.52	−66.7428	0.059
Georges Bank	10	41.0715	−68.2751	0.138
Mid-Atlantic	16	39.9782	−72.2489	0.128
Cape Hatteras	2	39.9782	−72.2489	0.153
Overall	31	—	—	0.139
Leucoraja erinacea				
Gulf of Maine	10	43.52	−66.7428	0.070
Georges Bank	17	41.0715	−68.2751	0.068
Mid-Atlantic	19	39.9782	−72.2489	0.067
Cape Hatteras	12	39.9782	−72.2489	0.073
Overall	57	—	—	0.077

Conservation implications and future work.—We found that both species of *Leucoraja* encompass only one breeding population, but that genetic variation is determined primarily by distance. Thus, range-wide genetic data would suggest that managers should consider each species as a single unit of conservation, rather than managing several populations. Although current management strategies for both species already utilize this approach (IUCN, 2016), we suggest two possible alternative management strategies. First, management efforts could focus on the areas of highest genetic diversity (Gentili et al., 2018). Using this strategy, managers would focus on conserving individuals from the southern localities of *L. ocellata,* which have the highest genetic diversity. If this strategy were employed with *L. erinacea*, conservation efforts would focus on the northern or southern localities, with fewer protections afforded central localities, which had lower genetic diversity. However, before this strategy was implemented for *L. ocellata,* sample sizes from the northern and southern localities would need to be increased and genetic diversity re-estimated.

Most species of skate are thought to exhibit philopatry, a life history characteristic that may favor sex-biased dispersal (Hueter et al., 2005). In this study, we lacked mitochondrial sequence data, and thus were unable to test for mitochondrial population structure. However, if females are philopatric in these species, mitochondrial haplotypes should exhibit some geographic structure. This simple hypothesis remains untested in this species and has considerable conservation implications (Pardini et al., 2001). However, as previous studies have demonstrated significant ecological and physiological differences in embryos and juveniles maintained under common garden conditions (Di Santo, 2015, 2016), we suggest that adults may travel widely between breeding events, but may return to natal sites to lay eggs (Lauder and Di Santo, 2015). Thus, the second conservation strategy would account for philopatry and an oviparous life history by focusing on essential habitats related to egg deposition and juvenile growth (Hoff, 2016). Conserving essential habitat would account for the spatial distribution of multiple life history

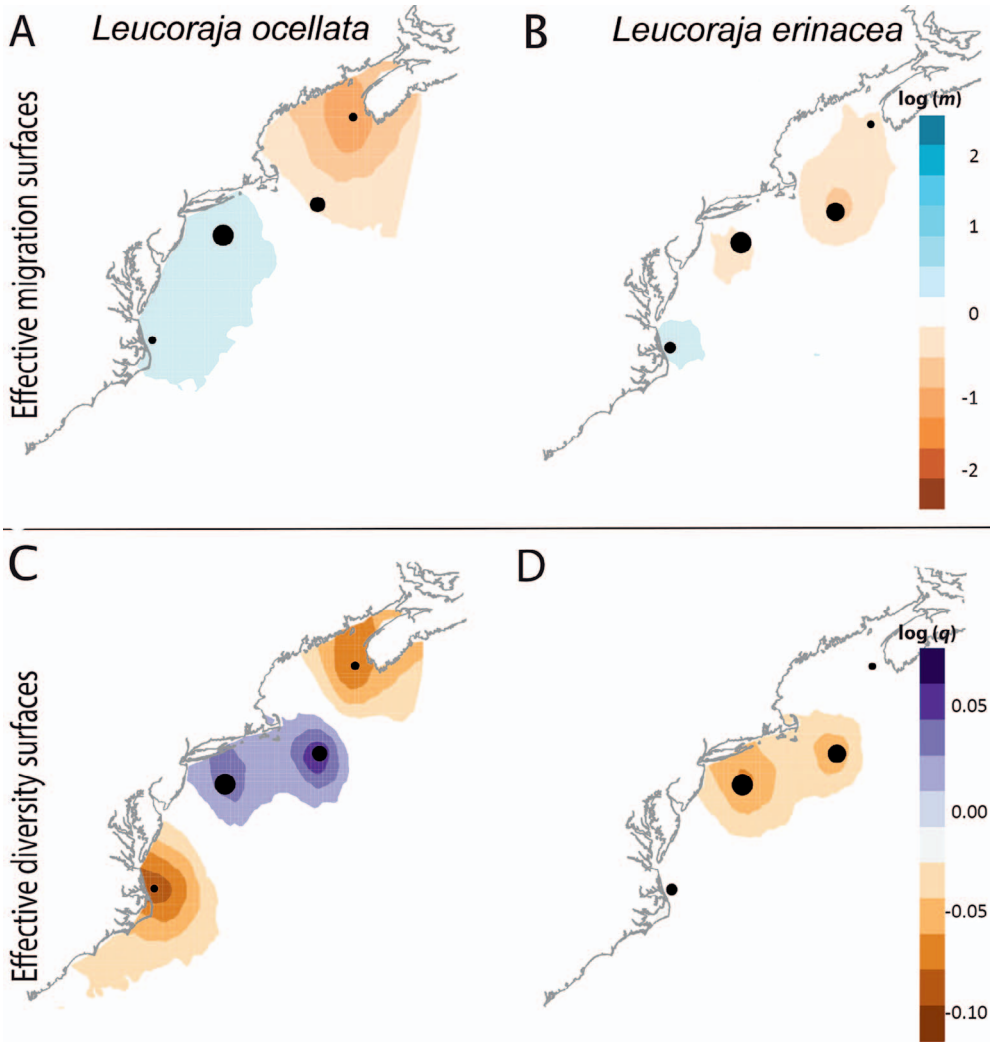

Fig. 4. Estimates of effective migration surfaces inferred by EEMS for *Leucoraja ocellata* (A) and *L. erinacea* (B). Blue colors represent estimated effective migration greater than that expected under isolation-by-distance, while orange colors represent barriers to movement. *Leucoraja ocellata* demonstrates fine-scale genetic structuring between northern and southern sites, while isolation by distance is inferred for *L. erinacea*. (C) Estimate of effective diversity surface for *L. ocellata* and (D) for *L. erinacea*. The distribution of genetic diversity is opposite in these species. Purple colors represent regions of elevated genetic diversity, while orange colors represent regions of depressed genetic diversity. Circles represent the four sampling localities in this study, and the size of the circles are proportional to the number of individuals included from that site that passed SNP filtering.

stages (Rosenberg et al., 2000; Hoff, 2016). Gold et al. (1999) proposed the concept of "geographic neighborhood" in which management actions are spatially structured among feeding, migratory, and reproductive sites. Although skates reproduce in coastal areas, under state jurisdiction, seasonal migrations are often in federal waters or cross state management boundaries. Effective protection and management practices may therefore consider separate strategies for reproductive, juvenile growth, adult migratory, and overwintering habitats.

DATA ACCESSIBILITY

Supplemental material is available at https://www.copeiajournal.org/cg-18-114.

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