High Rates of Genetic Polyandry in the Blacknose Shark, *Carcharhinus acronotus*

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Genetic polyandry was assessed in 27 litters of Blacknose Shark (*Carcharhinus acronotus*) from genetically distinct populations in the U.S. Atlantic (19 litters) and eastern Gulf of Mexico (eight litters) using 23 polymorphic microsatellite loci. Two methods were used to estimate genetic polyandry, and the overall observed rates were high (74% COLONY2; 81% allele counting method), with a maximum of four sires detected in a single litter. When separated by region, the rate of genetic polyandry was 63% (COLONY2) or 74% (allele counting method) in the U.S. Atlantic, and 100% (both methods) in the eastern Gulf of Mexico. Data were resampled to evaluate how the number and diversity of markers analyzed affected the estimated rate of genetic polyandry. The number of alleles per locus had a dramatic effect on the detection of polyandry, with a difference of 56% in the estimated rate of genetic polyandry (22% vs. 78%), when using only the five loci with the highest diversity (A = 21–44) versus lowest diversity (A = 3–5). The total number of markers assessed also affected the estimated rate of genetic polyandry, and the estimated rate increased by 13% when using 10 versus 20 loci (66% vs. 79%, respectively). These results suggest that unless loci are highly polymorphic, relatively large numbers of loci are required to estimate the rate of genetic polyandry accurately in elasmobranchs, particularly those with small litter sizes like the Blacknose Shark.

POLYANDRY is a reproductive strategy in which females mate with multiple males and may occur within breeding seasons (synchronous polyandry) or between breeding seasons (serial monogamy; Jennions and Petrie, 2000; Holman and Kokko, 2013; Taylor et al., 2014). Multiple paternity (genetic polyandry) occurs when a single brood is sired by more than one male. This has been documented across a variety of taxa, including reptiles (Uller and Olsson, 2008), birds (Griffith et al., 2002), mammals (Kitchen et al., 2006; Gottelli et al., 2007; Bergeron et al., 2011), and elasmobranchs (Byrne and Avise, 2012). Proposed benefits of genetic polyandry include increased realized fecundity, increased genetic diversity among offspring, inbreeding avoidance, and/or post-copulatory selection for the best or most genetically compatible sires (Zeh and Zeh, 1996, 1997; Jennions and Petrie, 2000; Foerster et al., 2003; Neff and Pitcher, 2004; Slatyer et al., 2011). Genetic polyandry is a common reproductive strategy in elasmobranchs (Byrne and Avise, 2012); however, evidence for such benefits has not been observed (Feldheim et al., 2004; Portnoy et al., 2007; DiBattista et al., 2008; Daly-Engel et al., 2010; Verissimo et al., 2010; Boomer et al., 2013). Instead, multiple mating by female elasmobranchs is thought to be a product of convenience polyandry (Portnoy et al., 2007), meaning that the costs associated with conceding to superfluous mating attempts are lower than the costs associated with avoiding additional mating. Therefore, the prevalence of genetic polyandry within a species or population may be a function of the contact frequency between the sexes (Daly-Engel et al., 2010), with higher rates of genetic polyandry associated with behaviors that increase encounters between males and females, such as aggregate mating and site fidelity to specific breeding grounds.

The Blacknose Shark (*Carcharhinus acronotus*) is a small coastal shark found in the western Atlantic, including the Gulf of Mexico (hereafter Gulf), from Virginia, USA to southern Brazil (Castro, 2011). *Carcharhinus acronotus* is targeted in both commercial and recreational fisheries (Hazin et al., 2002; Cortés and Neer, 2007), and is also caught as bycatch in offshore shrimp fisheries (Nichols, 2007). *Carcharhinus acronotus* reaches maturity between three and five years of age (Driggers et al., 2004; Sulikowski et al., 2007) and gives birth to litters of 3–6 fully developed pups (Compagno, 1984), following a gestation period of 9–11 months (Dodrill, 1977; Schwartz, 1984; Driggers et al., 2004; Sulikowski et al., 2007). Due to its relatively low lifetime fecundity and susceptibility to directed and non-directed fishing, *C. acronotus* has been assessed as near threatened throughout its range by the International Union for Conservation of Nature (Morgan et al., 2009) and is considered overfished with overfishing occurring in the U.S. Atlantic (SEDAR, 2011a, 2011b). Genetic analysis of stock structure revealed five distinct populations of *C. acronotus* in the northwest Atlantic: the U.S. Atlantic, the Bahamas, and the eastern, western, and southern Gulf (Portnoy et al., 2014).

Commensurate with these genetic differences, regional variation has been observed in reproductive biology between U.S. Atlantic and eastern Gulf populations of *C. acronotus*. In the Gulf, pupping is thought to occur from late May to the beginning of June, and neonates are found in nearshore waters off northern Florida (Grubbs, unpubl.). Based on examinations of reproductive tissues, mating likely occurs soon after parturition from May to July (Sulikowski et al., 2007), although mating grounds have not yet been identified. In the U.S. South Atlantic, mating has been observed coastally from late May to early June (Driggers et al., 2004), at which time adults and juveniles are abundant and found in

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large aggregations, not segregated by sex or size (Ulrich et al., 2007). The presence of juveniles in these aggregations suggests they do not function solely as mating aggregations, and it is unknown if discrete mating grounds exist. While the coastal waters of South Carolina have been proposed to act as nursery areas for *C. acronotus* (Castro, 1993), few neonates have been observed despite considerable sampling effort in this region (Driggers et al., 2004; Frazier, unpubl.), and pupping may not occur in discrete inshore habitat. Finally, female *C. acronotus* reproduce on annual or biennial cycles, but the prevalence of annual and biennial females appears to differ by region (Hazin et al., 2002; Driggers et al., 2004; Sulikowski et al., 2007).

In this study, the rate of genetic polyandry was assessed in *C. acronotus* sampled in the U.S. Atlantic and eastern Gulf, using 23 microsatellite loci. Given the prevalence of genetic polyandry in other elasmobranchs, multiple paternity would be expected in *C. acronotus*, but given regional differences in reproductive biology, there may also be differences in the rate of genetic polyandry. Given small litter sizes present in this species and other elasmobranchs, the data were resampled to evaluate the effect that the number of loci and the diversity of those loci had on the estimated rate of genetic polyandry.

MATERIALS AND METHODS

Fin clips were collected from 27 pregnant female *C. acronotus* and their litters captured via directed bottom longline fishing off the Florida Keys (8) and the U.S. Atlantic (19; Fig. 1) between 2011–2014. Tissues were stored in 20% DMSO buffer (Seutin et al., 1991) and DNA extractions were performed following a modified Chelex extraction protocol (Estoup et al., 1996). Previous genetic analyses indicated *C. acronotus* in the Florida Keys are distinct from the U.S. Atlantic, and group with the eastern Gulf of Mexico (Portnoy et al., 2014; Dimens et al., 2019); therefore, the Florida Keys will be referred to as the eastern Gulf. All individuals were genotyped at 23 microsatellite loci isolated from *C. acronotus* and Finetooth Shark *Carcharhinus isodon* (Giresi et al., 2012a, 2012b). Forward primers were labeled with one of three fluorescent dyes (6-FAM, HEX, NED; Applied Biosystems). PCR conditions followed those described by Portnoy et al. (2014). Amplicons were mixed with GeneScan™ 400 HD Rox™ Size Standard (Applied Biosystems) and resolved on a 6% polyacrylamide gel using an ABI Prism 377 sequencer (Applied Biosystems). Genotypes were scored manually using GENESCAN v. 3.1.2 (Applied Biosystems) and GENOTYPER v. 2.5 (PerkinElmer). Summary statistics for these loci have been previously reported elsewhere (Portnoy et al., 2014; Supplemental tables; see Data Accessibility).

Two methods were used to estimate the number of sires contributing to each litter. In the allele counting method, a manual inspection of genotypes was performed to confirm that each pup had a maternal allele at each locus. The number of paternal alleles within a litter was then summed and the number of sires assigned accordingly for each locus. The number of sires per litter (across loci) was determined by identifying the maximum number of sires supported by two or more loci. To complement the allele counting method, a likelihood approach was also used to construct groups of full siblings nested within groups of half-siblings (related through known, genotyped mothers) and reconstruct paternal genotypes, as implemented in the program Colony2 v. 2.0.6.4 (Jones and Wang, 2010). The mating system was set to female polygamy and male monogamy without inbreeding. Although males are likely polygamous as well, this parameter does not affect estimates of number of sires and reproductive skew within litters. Five runs were conducted using the full-likelihood analysis method with the medium run length option, an allele dropout rate of 0, and genotyping error/mutation rate of 0.01. Allele frequencies for each subpopulation were obtained from Portnoy et al. (2014), and analyses were run separately for litters sampled in the U.S. Atlantic and eastern Gulf due to differing allele frequencies in the two populations. Estimates of reproductive skew were also made by assessing the number of offspring sired by each male in multiply sired litters. Two likelihood probabilities are reported by Colony2 to indicate the extent to which families may be over- or under-split. A high inclusion probability indicates that a group of full siblings is likely to be real and should not be further split into half siblings (i.e., not under-split). A high exclusion probability indicates the full sibship is complete and no other individuals are likely to belong (i.e., not over-split). When a high inclusion probability is coupled with a low exclusion probability for a given family it suggests that while assigned full siblings are likely to be true full siblings, the sibship has probably been over-split and some half siblings are in reality full siblings, which leads to an overestimation of the number of sires.

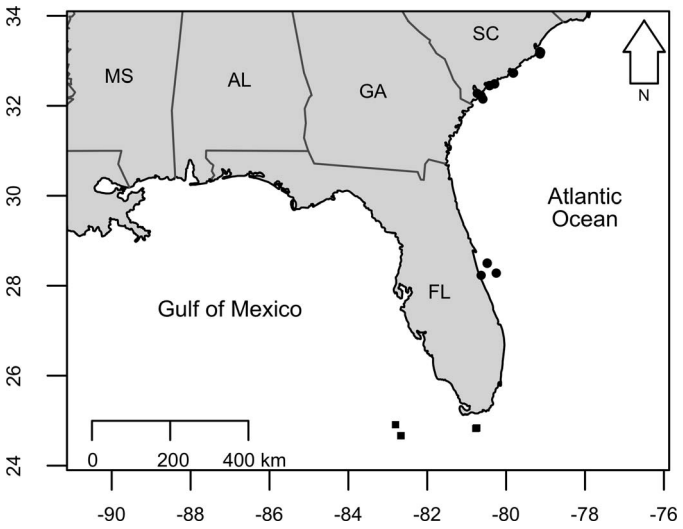

Fig. 1. Map of sampling locations in the U.S. Atlantic (circles) and Gulf of Mexico (squares).

The overall rate of genetic polyandry was calculated by dividing the number of multiply sired litters obtained from each method by the total number of litters sampled. In addition, the rate of genetic polyandry was calculated separately for the U.S. Atlantic and eastern Gulf to evaluate intraspecific variation between populations. To determine whether differences between the eastern Gulf and U.S. Atlantic were significant, a two-sided Barnard's test (Barnard, 1947) was run using the R package *Barnard* (Erguler, 2016). In addition, an R simulation was run to calculate the probability that differences observed between the regions were an artifact of the small numbers of litters obtained from the eastern Gulf ($n = 8$), relative to the U.S. Atlantic ($n = 19$). Briefly, eight litters were assigned as either sired by a single male or multiple males, with the probability determined by the estimated rate of genetic polyandry in the Atlantic. This was repeated for 100,000 iterations and the frequency that

the rate of genetic polyandry in simulated litters equaled the estimate for the eastern Gulf was calculated.

To evaluate the effect that the number of loci deployed had on estimated rates of genetic polyandry, a python script was used to calculate the estimated number of sires using the allele counting method from a subset of microsatellite loci using the empirical data. Briefly, the rate of genetic polyandry was calculated for all 23 loci individually and averaged to get the mean estimated rate of genetic polyandry when one locus was analyzed. Then, the rate of genetic polyandry was calculated for every possible combination of two loci and averaged to get the mean estimated rate of genetic polyandry when two loci were analyzed. Using the same procedure, mean estimates were then generated for 3–23 loci. As with the allele counting method described above, genetic polyandry had to be supported by at least two loci, with the exception of the estimations generated from one locus. To evaluate the effect that marker polymorphism had on estimated rate of genetic polyandry, the script was run separately on a data set containing the five loci with the highest allelic diversity (A = 21–44) and a data set containing the five loci with lowest allelic diversity (A = 3–5), as determined by allelic diversity data from Atlantic and western Gulf subpopulations from Portnoy et al. (2014; Supplemental Table 1; see Data Accessibility).

The program PrDM calculates the probability of detecting multiple mating given population allele frequencies, litter size, the number of sires and their reproductive skew, and the mother's genotype, if available (Neff and Pitcher, 2002), and is commonly used to demonstrate adequate power to estimate rates of genetic polyandry (e.g., Daly-Engel et al., 2007; Byrne and Avise, 2012; Rossouw et al., 2016). Therefore, the effect that the number of loci has on the results of PrDM was also assessed using a python wrapper script. The loci *Cac40* and *Cac*67 were excluded because PrDM analysis is limited to 30 alleles per locus and Portnoy et al. (2014) observed 44 and 32 alleles at these loci, respectively. PrDM was used to assess the probability of detecting two sires with equal (50:50) and unequal (75:25) reproductive skew. PrDM was not calculated for three or more sires, as genetic polyandry becomes easier to detect as the number of sires increases. First, PrDM was run for each litter with one randomly selected locus. Loci were randomly selected using the function *random.sample* from the *random* python library. Next, PrDM was run for each litter with two randomly selected loci. Each consecutive run was conducted with a new set of randomly selected loci, increasing the number of loci by one. Finally, PrDM was averaged across all litters for each number of loci (1–21). This procedure was repeated for 100 iterations, and PrDM averaged across all iterations for each number of loci. The exhaustive, combinational approach utilized in the paternity assessment simulation could not be repeated with PrDM due to computational limitations.

RESULTS

A total of 108 offspring from 27 litters were genotyped at 23 microsatellite loci. Litter sizes ranged from three to six pups, with an average litter size of four pups. The overall rate of genetic polyandry differed slightly between the two methods. The estimated rate of genetic polyandry (allele counting method) was 81% (22/27) and the number of sires ranged from one to three (Table 1), with an average of 1.89 sires per litter. Litters M17 and M22 had more than two paternal alleles at a single locus, but genetic polyandry was not supported by any additional loci and thus each were conservatively considered to be sired by a single male. Colony2 results indicated 20/27 litters (74%) were multiply sired, with the number of sires ranging from one to four, and an average of 2.44 sires per litter. Reproductive skew was variable, with a single male accounting for as much as 75% of the pups within a litter (Table 1). Overall inclusion probabilities for our data were generally high; out of 66 reported full sibships, only four had an inclusion probability less than 0.90 (range 0.56–1.00, average 0.98). Exclusion probabilities were more variable, with 22/66 less than 0.90 (range 0.26–1.00, average 0.88), suggesting some overestimation of the number of sires. Although Colony2 results suggest an overall lower rate of genetic polyandry than the allele counting method, broods that were identified as being multiply sired were generally attributed to more sires by Colony2 (Table 1).

Table 1. Summary of litter data and paternity results, including litter size, sampling location, number of sires estimated by the allele counting method (AC), number of sires estimated by Colony2 (COL), and reproductive skew (Skew) as determined by Colony2.

Litter	Litter size	Location	AC	COL	Skew
M01	5	E. Gulf	2	3	3:1:1
M02	4	E. Gulf	2	3	2:1:1
M03	3	E. Gulf	2	3	1:1:1
M04	4	E. Gulf	2	3	2:1:1
M05	3	E. Gulf	2	2	2:1
M06	3	E. Gulf	2	2	2:1
M07	3	E. Gulf	2	3	1:1:1
M08	4	E. Gulf	2	3	2:1:1
M09	6	U.S. Atlantic	3	4	3:1:1:1
M10	4	U.S. Atlantic	2	2	3:1
M11	4	U.S. Atlantic	1	1	–
M12	3	U.S. Atlantic	2	2	2:1
M13	4	U.S. Atlantic	2	3	2:1:1
M14	4	U.S. Atlantic	2	3	2:1:1
M15	6	U.S. Atlantic	1	1	–
M16	3	U.S. Atlantic	2	1	–
M17	3	U.S. Atlantic	1	1	–
M18	4	U.S. Atlantic	2	3	2:1:1
M19	4	U.S. Atlantic	2	3	2:1:1
M20	5	U.S. Atlantic	3	4	2:1:1:1
M21	5	U.S. Atlantic	2	3	2:2:1
M22	4	U.S. Atlantic	1	1	–
M23	4	U.S. Atlantic	2	4	1:1:1:1
M24	4	U.S. Atlantic	2	1	–
M25	4	U.S. Atlantic	1	1	–
M26	3	U.S. Atlantic	2	3	1:1:1
M27	5	U.S. Atlantic	2	3	2:2:1

Variation in the rate of genetic polyandry was observed between the U.S. Atlantic (74%; allele counting method, 63%; Colony2) and eastern Gulf (100%, both methods). In the U.S. Atlantic, the number of sires ranged from 1–3 (average 1.84; allele counting method) or 1–4 (average 2.47; Colony2). In the eastern Gulf, there were two sires for each litter (allele counting method) or 2–3 (average 2.75; Colony2). The Barnard's test did not indicate a significant difference in the number of multiply sired litters between eastern Gulf and U.S. Atlantic, using results from the allele counting method ($P = 0.06$, Wald statistic = 2.60), but the test was significant when the number of multiply sired litters was

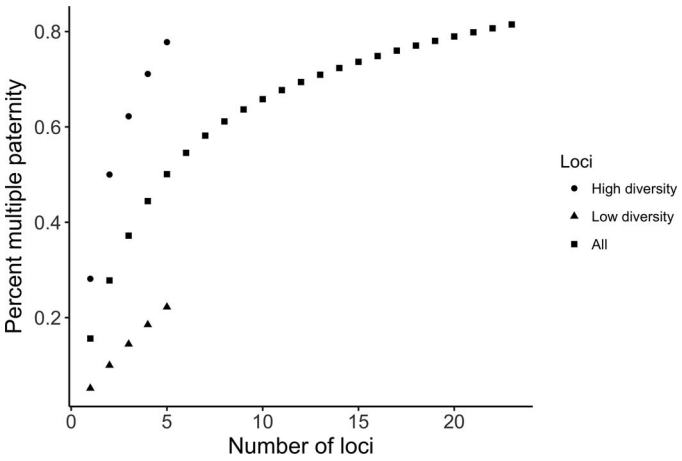

Fig. 2. Result of paternity simulation showing the percentage of litters sired by multiple fathers when all loci were analyzed (All; average no. alleles = 13.8), five loci with highest diversity (High diversity; average no. alleles = 29.6), and five loci with lowest diversity (Low diversity; average no. alleles = 4.4).

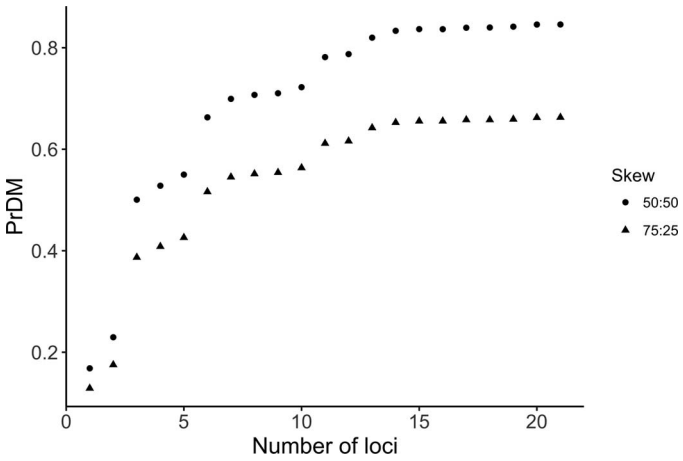

Fig. 3. Results of PrDM simulation showing the probability of detecting multiple paternity given different numbers of loci and reproductive skew.

based on COLONY2 ($P = 0.02$, Wald statistic = 3.33). Results of the simulation indicated that the probability that 100% genetic polyandry would be observed in the eastern Gulf by chance, given the small sample size, was 2.5% if the true rate was 63%, and 9% if the true rate was 74%.

The number of loci used had a clear effect on the estimated rate of genetic polyandry, with the final estimated rate of 81% not reached until all 23 loci were used (Fig. 2). The difference in the estimated rate of genetic polyandry between 10 and 20 loci was 13% (66% and 79%, respectively). Diversity of the markers deployed also had a marked effect on the detection of genetic polyandry. When the five loci with the highest number of alleles were used (A = 21–44; average = 29.6), the estimated rate of genetic polyandry was 78%. When the five loci with the fewest number of alleles were used (A = 3–5; average = 4.4), the estimated rate of genetic polyandry was 22%. The averaged probability of detecting multiple mating reached an asymptote at 15 loci, regardless of the degree of reproductive skew (Fig. 3). With a 50:50 reproductive skew, the difference in probability between 10 and 20 loci was 0.72 vs. 0.84, respectively, and for a 75:25 reproductive skew, the difference in probability was 0.56 vs. 0.66, respectively.

DISCUSSION

This study is the first to demonstrate the occurrence of genetic polyandry in *C. acronotus* and provides further evidence that genetic polyandry is widespread in elasmobranchs. The rate of genetic polyandry in *C. acronotus* reported here (74–81%) is on the high end of what has been observed in other carcharhinids, which has been as low as 35% in the Dusky Shark *C. obscurus* (Rossouw et al., 2016) and as high as 85% in the western North Atlantic population of the Sandbar Shark *C. plumbeus* (Portnoy et al., 2007).

Considerable intraspecific variation in rates of genetic polyandry in sharks has been reported between studies. The estimated rate of genetic polyandry for *C. plumbeus* in Hawaii (40%; Daly-Engel et al., 2007) was less than half the estimated rate in the western North Atlantic and Gulf of Mexico (85%; Portnoy et al., 2007). Similarly, rates of 46% (southern Africa; Rossouw et al., 2016) and 100% (Papua New Guinea; Green et al., 2017) have both been reported for the Scalloped Hammerhead *Sphyrna lewini*, and 17% (Verissimo et al., 2010) and 30% (Lage et al., 2008) for Spiny Dogfish *Squalus acanthias* in the western North Atlantic. Temporal and spatial variation has been reported for the Brown Smoothhound Shark *Mustelus henlei*, with 93% genetic polyandry in Baja California Sur, Mexico (Byrne and Avise, 2012), while rates of 0% and 40% were observed off Santa Catalina Island, California, across different sampling years (Chabot and Haggin, 2014). While eastern Gulf sample size was relatively low compared to the Atlantic and statistics varied depending on the method used to detect polyandry, the probability that observed differences were due to chance was low, suggesting that the results may represent another example of spatial heterogeneity in rates of genetic polyandry.

The intraspecific variation in rates of genetic polyandry (and average number of sires per litter) coincides with documented differences in reproductive biology between the regions, and this may provide insight into the mechanisms favoring synchronous genetic polyandry in *C. acronotus*. If multiple mating provides direct benefits for females, there should be an increase in realized fecundity associated with the number of sires (Jennions and Petrie, 2000; Slatyer et al., 2011). Contrary to this idea, both the rate of genetic polyandry and average sires per litter in the Atlantic (63–74% and 1.84–2.47, respectively) were smaller than in the Gulf (100% and 2.00–2.75, respectively), even though the average litter size in the Atlantic (4.16) was larger than the Gulf (3.63). While the average litter sizes observed in this study were based on a small number of litters, precluding rigorous statistical assessment, previous research also found smaller average litter sizes in the Gulf (3.13) than the Atlantic (3.53; Driggers et al., 2004; Sulikowski et al., 2007).

It has been suggested that multiple mating provides increased genetic variance among progeny for females with limited lifetime mating opportunities (Jennions and Petrie, 2000; Kempenaers, 2007; Slatyer et al., 2011). In the Atlantic, females mature at 4.5 years and have a maximum estimated age of 20.5 (Driggers et al., 2004; Frazier et al., 2015), whereas in the Gulf, females mature at 6.6 years with a maximum estimated age of 11.5+ (Carlson et al., 2007; Sulikowski et al., 2007; Frazier et al., 2015). While differences in estimates of longevity between the regions may be due in part to small sample sizes in the Gulf (Carlson et al., 2007), there is a

general trend that suggests small coastal sharks have greater longevity in the Atlantic than the Gulf (e.g., Carlson and Baremore, 2003; Frazier et al., 2014, 2015). Further, female *C. acronotus* in both the Atlantic and Gulf have been observed to exhibit both annual and biennial reproductive cycles with similar frequency (Hendon et al., 2014; Gelsleichter, unpubl.). Taken as a whole, these reproductive differences suggest that females in the Gulf have lower lifetime opportunity for reproductive effort, producing less offspring per lifetime than females in the Atlantic. Consistent with the increased genetic variance hypothesis, females in the Gulf have a higher rate of genetic polyandry.

Factors that contribute to the ability to detect genetic polyandry within a litter include the number of offspring, reproductive skew, the number of loci deployed and marker polymorphism (Neff and Pitcher, 2002; Sefc and Koblmüller, 2008). The first two parameters are controlled by the reproductive biology of the organism; therefore, researchers can only improve power by using more markers or screening a large number of markers to characterize those with sufficiently high polymorphism. Most elasmobranchs have low numbers of offspring per litter, and elasmobranch paternity studies have generally used five to ten microsatellite loci (see Rossouw et al., 2016), with evidence of genetic polyandry found using as few as four loci (Chapman et al., 2004; Byrne and Avise, 2012; Nosal et al., 2013; Chabot and Haggin, 2014). The results of this study verify that a single locus would have been sufficient to determine that at least some *C. acronotus* mate multiply. However, correctly estimating the rate of genetic polyandry required sampling more than 20 loci (when per-locus diversity was not considered) and estimates made with samples of ten loci, typical of many studies, were off by nearly 13%. In fact, the final estimated rate of genetic polyandry (81%) was not reached until all 23 loci had been used, despite the fact that PrDM suggested overall, little additional power was gained beyond the use of 15 loci.

In conjunction with the number of loci used, allelic diversity also had an effect on the ability to detect genetic polyandry. When the five least diverse loci were used (average A = 4.4), the estimated rate of genetic polyandry was 22%, but when the five most diverse loci were used (average A = 29.6), the estimated rate of genetic polyandry was close to the rate estimated when all loci were used (78% and 81% respectively). In practice, such high average allelic diversity across five loci is unlikely for elasmobranch studies, unless a large panel of markers is screened. Rossouw et al. (2016) compiled a table of 28 studies that assessed genetic polyandry in elasmobranchs and the average number of markers deployed was 7.4. Of the 21 studies listed that used at least five loci, the average allelic richness of the five most diverse loci ranged from 3.8–34.8 (average 13.6). A qualitative assessment of this table reveals that studies reporting high rates of genetic polyandry generally had relatively high marker diversity and/or assessed a relatively large number of markers (Supplemental Data; see Data Accessibility). Marker diversity may be particularly important when assessing interspecific variation in rates of genetic polyandry and could potentially explain differences in estimates for *C. plumbeus* (85% vs. 45%; Daly-Engel et al., 2007; Portnoy et al., 2007) and *S. lewini* (100% vs. 46%; Rossouw et al., 2016; Green et al., 2017); the studies that reported higher rates of genetic polyandry had higher average marker diversity. The move towards next-generation sequencing and large datasets is not yet commonplace in elasmobranch research, but for paternity studies, these methods would allow for very accurate estimates of paternal contribution.

Despite small litter sizes, high rates of genetic polyandry in *C. acronotus* were observed, and in part this may be due to the large number of microsatellites available, including some with very high levels of polymorphism. Our results suggest an underestimation of genetic polyandry rates may be present in the elasmobranch literature if too few loci with insufficient levels of polymorphism are deployed, given the small litter sizes found in many species. Finally, our results add to the growing list of studies that find no conclusive evidence for a benefit to multiple mating, suggesting that convenience polyandry and contact rates may govern patterns of genetic polyandry in elasmobranchs rather than direct or indirect benefits.

DATA ACCESSIBLITY

Data and scripts are available at https://github.com/ambarker/Blacknose_paternity. Supplemental material is available at https://www.copeiajournal.org/cg-19-180.

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