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Genetic evidence for regional philopatry of the Bull Shark (*Carcharhinus leucas*), to nursery areas in estuaries of the Gulf of Mexico and western North Atlantic ocean

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ABSTRACT

Nursery areas are critical for the reproductive cycle and biological requirements of Bull Sharks (*Carcharhinus leucas*) as they increase the survival of populations. Females tend to be philopatric to these areas as documented in estuaries from Australia, and inferred in the northern Gulf of Mexico and western North Atlantic Ocean, but not yet confirmed in these region. In coastal waters of the southeastern United States, several sites have been proposed as nurseries for the Bull Shark, but little is known about how adult females utilize these areas during parturition. Philopatry for the Bull Shark was evaluated by comparing sequences of the mitochondrial DNA control-region (mtDNA-CR) and 8 microsatellite *loci* in juveniles and neonates from four previously reported nursery areas in United States (US) coastal waters; three in the northern Gulf of Mexico (Texas, Louisiana and Charlotte Harbor, Florida) and one in the western North Atlantic Ocean (Indian River Lagoon, Florida). A group of adult individuals from the Gulf of Mexico and Atlantic Ocean off the southeastern US were used to test genetic differences owed to limited gene flow between both regions. The analysis of genetic variation with the mtDNA-CR showed no differences among nurseries within the Gulf but significant differences when comparing the nursery areas of the two regions (Gulf vs Atlantic). In contrast, genetic homogeneity was observed among nursery areas within and between regions with the nuclear microsatellites suggesting male biased dispersal among regions. In addition, adult individuals from each of these two broad regions (Gulf of Mexico and Atlantic Ocean) showed no significant differentiation with any of the markers characterized in this study. These patterns of genetic differences support evidence for philopatry, further relaying the importance of protection and effective management of critical nursery habitats for future conservation of the species.

1. Introduction

The Bull Shark is a cosmopolitan coastal species with late sexual maturation and a long pregnancy (~10–11 months; Compagno, 1984) that uses estuarine and freshwater nursery areas to enhance its survival (Curtis et al., 2011; Heupel and Simpfendorfer, 2011). Offspring typically inhabit these areas for extended periods of time (Thorburn and Rowland, 2008; Curtis et al., 2011) away from most predators, and with suitable prey availability. Regional philopatry for females has been documented in nurseries from Australia (Tillett et al., 2012), and used (although not strictly confirmed) to explain genetic differences between samples from the northern Gulf of Mexico and Atlantic (Karl et al. 2011). This evidence highlights the importance of properly characterizing the nursery areas for Bull Sharks throughout its worldwide range.

In coastal waters of the southeastern United States, multiple sites have been proposed as nursery areas for the Bull Shark based on studies that aimed to unravel the dynamics of neonates and juveniles within the estuaries they inhabit. These nurseries include estuaries along the coasts of Florida, Louisiana and Texas (Simpfendorfer et al., 2005; Curtis et al., 2011; Blackburn et al., 2007; Froeschke et al., 2010a,b),

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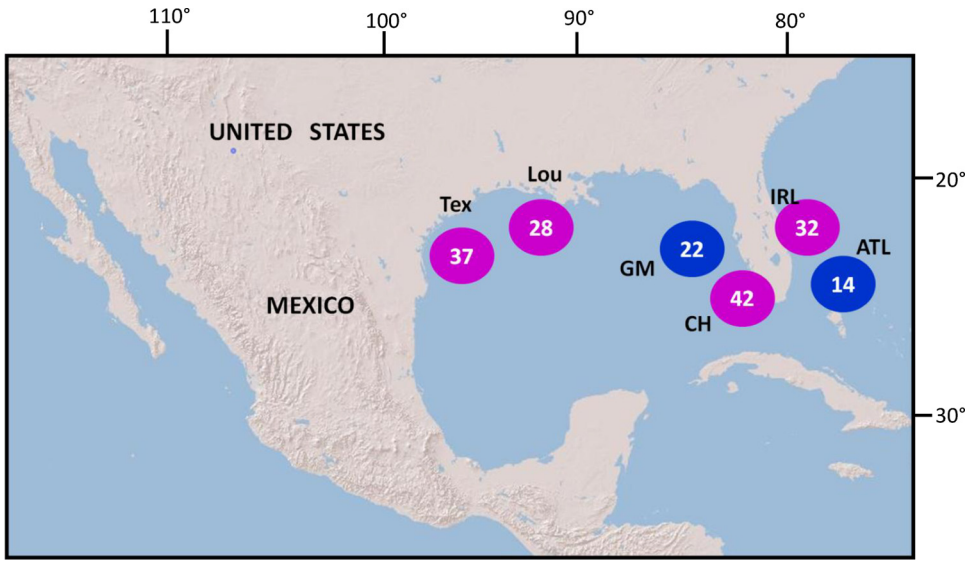

Fig. 1. Sample locations and number of Bull Shark individuals sampled from the Gulf of Mexico and Atlantic Ocean. Adults are in blue circles and juvenile individuals are in pink. Nurseries are Lou (Louisiana), Tex (Texas), CH (Charlotte Harbor, Florida) and IRL (Indian River Lagoon, Florida). Adult individuals were collected from the Atlantic (ATL) and Gulf of Mexico (GM) coasts of Florida (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

but little is known about how adult females utilize these areas while giving birth, since the number of tagged adults in these areas is very low (Carlson et al., 2010; Brunnschweiler et al., 2010) and there is only one genetic study that characterized Bull Shark samples from different localities in the Gulf of Mexico and the Atlantic (Karl et al., 2011). To date, the genetic variability of juveniles among the different nursery areas found along the southeastern coast of the US is unknown, but differences in catches based on the analysis of fisheries data (Curtis et al. 2011) together with the potential philopatry of females towards birthing areas, suggest the possibility that genetic differences may exist.

Nursery areas are critical zones where gravid females of coastal shark species give birth and where their young spend their initial period of life which may last from a few weeks up to several years in length (Castro, 1993). Such sites are identified because of the remarkable abundance of neonate/juveniles, long residence times, and repeated use as compared to nearby non-nursery areas (Heupel et al., 2007). Additionally, females of several shark species (e.g. Lemon Shark *Negaprion brevirostris*; Blacktip Shark *Carcharhinus limbatus*; Scalloped Hammerhead *Sphyrna lewini,* and Sandbar Shark *Carcharhinus plumbeus*) tend to display philopatric behaviour to specific sites which are also used as birthing areas (Hueter, 1998; Hueter et al., 2005; Chapman et al., 2015). Regional philopatry in the present study is classified as the repeated utilization of a specific nursery region by adults for reproduction, but not necessarily to a specific birthing area within that region (see Chapman et al., 2015).

In general, philopatry would result in genetic differences between sites at a regional scale whereas for specific (or natal) philopatry these differences would be at small scales (Tillett et al., 2012, Feldheim et al., 2014) for the maternally inherited mitochondrial DNA haplotypes. However such differences may not be replicated by characterizing biparentally inherited nuclear DNA loci, as has been reported for many marine species (Rassmann et al.,1997; Lyrholm et al., 1999; Pardini et al., 2001; Engelhaupt et al., 2009), including an increasing number of shark species known to display philopatric behaviour in some regions (Hueter et al., 2005; Chapman et al., 2015), such as the Bull Shark *Carcharhinus leucas* (Karl et al., 2011; Tillett et al., 2012), the Blacktip Shark *Carcharhinus limbatus* (Keeney et al., 2005) and the Scalloped Hammerhead *Sphyrna lewini* (Chapman et al., 2009).

Sharks tend to be species with low reproductive potential due to late maturity and low fecundity and are more likely to suffer severe population reductions caused by overfishing, habitat degradation and other factors (Musick et al., 2000; Dulvy et al. 2014). Many shark species currently lack data regarding key biological parameters, fisheries landings, and population status that are required to design effective conservation strategies. An estimated one-quarter of the world's chondrichthyan fishes (including sharks, rays, skates, and chimaeras) are classified as threatened (Dulvy et al., 2014). To safeguard the survival of shark species, it is necessary to develop directed conservation strategies that include measures to protect vulnerable early life-history stages. Accordingly, the proper identification, delineation, and management of nursery areas are crucial for the conservation of the species that use them (Heithaus, 2007).

Significant commercial and recreational fisheries for carcharhinid sharks, including Bull Sharks, have occurred in US Atlantic waters for many decades but increased in the mid-1980's. Bull Sharks typically represent a small percentage of total large coastal shark landings in the US Atlantic, however landings of this species can be variable (Morgan et al., 2009; NMFS, 2012). The International Union for Conservation of Nature (IUCN) has categorized the Bull Shark as "Near Threatened" worldwide. Fisheries-dependent data infer an estimated 12% increase in relative abundance of Bull Sharks in the western North Atlantic from 1994 to 2009 (Carlson et al., 2012) and increased juvenile abundance in estuarine waters of Texas (Froeschke et al., 2010a,b), although local population decreases have also been reported (O'Connell et al., 2007). The stock status of this species in US waters is not known (NMFS, 2006).

In order to evaluate the hypothesis of philopatric behaviour for female Bull Shark in the northern Gulf of Mexico and US Atlantic waters, the genetic divergence among sites was compared using mtDNA-CR sequences and nuclear DNA microsatellite markers, in samples of immature individuals from four different nursery areas and also verified the genetic signal for adults in adjacent offshore waters. Our sampling design and methodological approach provides evidence of philopatry toward nurseries as the most probable explanation of the genetic differences we observed.

2. Materials and methods

2.1. Sample collection and DNA extraction

Tissue samples (fin clips and muscle) from a total of 175 Bull Shark specimens were collected (Fig. 1), with 139 of these from neonates or small juveniles (immature sharks) obtained of four different nurseries within two main regions in US waters; three in the northern Gulf of Mexico at Sabine Lake, Texas (Tex: n = 37); Lake Pontchartrain, Louisiana (Lou: n = 28); and Charlotte Harbor, Florida (CH; n = 42) and one in the western North Atlantic Ocean within the Indian River Lagoon, Florida (IRL; n = 32). Individuals were considered neonates