



Full length article

## Population structure of istiophorid billfishes

John E. Graves\*, Jan R. McDowell



Virginia Institute of Marine Science, College of William &amp; Mary, 1375 Greate Rd., Gloucester Point, VA 23062, USA

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### ABSTRACT

The phylogeny of istiophorid billfishes was recently revised based on analyses of nuclear and mitochondrial DNA loci, and a variety of molecular genetic characters has been used to investigate population structuring within several species of billfish. Despite these efforts, the population structure of most istiophorid billfishes is not well understood. This paper reviews genetic insights into the phylogeny and population structure of the billfishes with an emphasis on recent studies. In general, the results of genetic studies indicate significant heterogeneity between Atlantic and Indo-Pacific samples of circumtropical species. Within ocean basins, levels of population structure range among the species from no statistically significant heterogeneity detected among samples to small, but statistically significant genetic divergence between geographically distant samples. The apparent high level of genetic connectivity within oceans for some species seems to contrast with inferences derived from studies employing conventional and satellite tags that suggest limited trans-equatorial or trans-oceanic movements. This disparity may result, in part, from the different time scales underpinning evolutionary and ecological population structure; however, the power of previous genetic studies to elucidate population structuring has been limited by opportunistic sampling. To effectively assess population structure within the highly migratory billfishes, future genetic research will not only require larger sample sizes, both in terms of individuals and molecular markers, but also the development of biologically meaningful sampling designs that incorporate information on the movement patterns and life histories of these pelagic fishes.

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### 1. Introduction

Billfishes of the family Istiophoridae are pelagic fishes that occur throughout the world's tropical and subtropical marine waters. The epipelagic environment in which they live is characterized by a lack of physical barriers, and the broad ranges and high dispersal abilities of these fishes tend to promote gene flow and erode population structure (Palumbi, 1994; Graves, 1998). NRM: In addition, most species are reported to spawn over broad geographic areas and over a prolonged season (Nakamura, 1985).

The lack of barriers to gene flow in the epipelagic realm would be expected to limit genetic population structuring and speciation of the billfishes (Graves and McDowell, 2003). In fact, there are only nine extant species of istiophorid billfishes. Two species, the blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*), are distributed circumtropically, and three species, the black marlin (*Istiompax indica*), striped marlin (*Kajikia audax*), and shortbill spearfish (*Tetrapturus angustirostris*), are broadly distributed throughout the Pacific and Indian oceans. The white

marlin (*Kajikia albida*), longbill spearfish (*Tetrapturus pfluegeri*), and roundscale spearfish (*Tetrapturus georgii*) occur throughout the Atlantic Ocean, while the Mediterranean spearfish (*Tetrapturus belone*) appears to be restricted primarily to the Mediterranean Sea. Billfishes are targeted in several small-scale artisanal fisheries, recreational fisheries, and represent a significant bycatch of pelagic longline fisheries for tunas and swordfish. Several species of billfishes are threatened by over-exploitation, especially the blue marlin and white marlin (Collette et al., 2011).

A variety of techniques has been used to investigate population structuring within several species of billfish, with the majority of inferences resulting from studies using conventional tagging or genetic analyses. In general, these studies have demonstrated relatively low levels of population structuring, consistent with the high dispersal ability of these fishes in a relatively homogeneous epipelagic environment. The results of conventional tagging studies and genetic studies of billfishes were last reviewed at the Third International Billfish Symposium in 2001 (Ortiz et al., 2003; Graves and McDowell, 2003), and the taxonomy and phylogeny of istiophorid billfishes was revised at the Fourth International Billfish Symposium in 2005 (Collette et al., 2006). In this paper we consider those studies that have contributed to our understanding of billfish phylogeny and population structure since those reviews,

\* Corresponding author. Tel.: +1 804 684 7352; fax: +1 804 684 7157.  
 E-mail address: [graves@vims.edu](mailto:graves@vims.edu) (J.E. Graves).

and compare insights from population genetic analyses with those from conventional tagging studies. In addition, we consider factors that may be limiting insights gained from population genetic analyses, and provide recommendations for future studies.

## 2. Billfish phylogeny

Nakamura (1985) recognized three genera and ten or eleven species within the Istiophoridae: *Makaira* comprised three species, the Atlantic blue marlin (*M. nigricans*), the Pacific blue marlin (*M. mazara*), and the black marlin (*M. indica*); *Istiophorus* consisted of two species, the Atlantic sailfish (*I. albicans*) and the Indo-Pacific sailfish (*I. platypterus*); and *Tetrapturus* was represented by five species, the striped marlin (*T. audax*), the white marlin (*T. albidus*), the shortbill spearfish (*T. angustirostris*), the longbill spearfish (*T. pfluegeri*), and the Mediterranean spearfish (*T. belone*), with the roundscale spearfish (*T. georgii*) being of questionable status. The validity of separate Atlantic and Indo-Pacific species of blue marlin and sailfish was questioned following genetic analyses that revealed minimal genetic divergence between ocean populations (Finnerty and Block, 1992; Graves and McDowell, 1995). Based on an analysis of three mitochondrial gene regions and a nuclear gene region, Collette et al. (2006) revised the Istiophoridae to include five genera and nine species. In the analysis, *Makaira* was not monophyletic and comprised two genera, *Makaira* and *Istiompax*. *Makaira* was represented by a single, circumtropical blue marlin (*M. nigricans*) that was sister to *Istiophorus*, and the placement of *Istiompax*, which comprised the black marlin (*I. indica*), was unstable. A single, circumtropical species of sailfish was recognized within *Istiophorus* (*I. platypterus*). *Tetrapturus* was also recognized as polyphyletic and considered to represent two monophyletic genera, *Tetrapturus* and *Kajikia*. *Kajikia* comprised two species, the striped marlin (*K. audax*) and the white marlin (*K. albidus*), and *Tetrapturus* consisted of four species of spearfish: the shortbill spearfish (*T. angustirostris*), the longbill spearfish (*T. pfluegeri*), the Mediterranean spearfish (*T. belone*), and the roundscale spearfish (*T. georgii*), which was validated by Shivji et al. (2006).

While there have not been any studies directly focused on the phylogeny of the Istiophoridae since the revision of Collette et al. (2006), the results of two recent genetic studies of billfishes can be used to evaluate their hypotheses. Hanner et al. (2011) reported on a mitochondrial DNA (mtDNA) barcoding study of istiophorid and xiphiid billfishes. They sequenced the mitochondrial COI gene region from 296 individuals, and included an additional 57 sequences from the literature. They also sequenced the nuclear rhodopsin gene for 72 individuals. Their results for both the COI and rhodopsin analyses supported the splitting of *Makaira* into *Makaira* and *Istiophorus* as well as the division of *Tetrapturus* into *Tetrapturus* and *Kajikia*. Analyses of these gene regions also reinforced the close genetic relationships of striped and white marlin within *Kajikia*, and the four spearfishes within *Tetrapturus* (Graves and McDowell, 1995; Collette et al., 2006). Consistent with the results of previous studies, neither gene region was able to resolve the species within either of these genera. Within *Kajikia*, 91 COI sequences, 44 from white marlin and 28 from striped marlin, resulted in 21 distinct haplotypes. Sequences from the two species were very similar; the between-group mean Kimura 2-parameter distance was 0.004 and in one case, the two species shared an identical haplotype (sequence). Results based on sequencing of the nuclear rhodopsin gene region, which included 22 striped marlin and 9 white marlin, had a single fixed nucleotide position that discriminated the majority of white and striped marlin; however, four striped marlin appeared to be heterozygous at this nucleotide position. Within *Tetrapturus*, 64 samples including 11 shortbill spearfish, 15 Mediterranean spearfish, 51 roundscale spearfish and

43 longbill spearfish COI sequences were examined resulting in 16 haplotypes, three of which were shared by two of the three species (Mediterranean + longbill, 2 shared haplotypes; Mediterranean + shortbill, 1 shared haplotype). Sequencing of rhodopsin from 27 samples including 10 roundscale spearfish, 7 longbill spearfish, 8 Mediterranean spearfish and two shortbill spearfish also failed to resolve these species. However, it is important to note that neither the COI nor the rhodopsin locus are known to be highly variable and therefore, given that billfishes are an evolutionarily recent group, examination of markers with a higher mutation rate is warranted.

The second study by Bernard et al. (2013) surveyed sequence variation at a more variable mitochondrial ND4L-ND4 gene region to investigate the distribution of roundscale spearfish within the Atlantic Ocean. Their analysis included sequences from other species of istiophorid billfishes and the topology of the resulting maximum likelihood tree was consistent with that of Collette et al. (2006). As with previous studies, neither white and striped marlin nor longbill and Mediterranean spearfish were resolved. This study did not include shortbill spearfish samples.

More research is needed to fully resolve the phylogeny of the Istiophoridae. The placement of *Istiompax* relative to the other genera remains problematic. White marlin and striped marlin are genetically very similar (Graves, 1998; Graves and McDowell, 2003) and were not resolved by Collette et al. (2006), Hanner et al. (2011), or Bernard et al. (2013). Similarly, there is a lack of resolution among the four spearfishes. Analysis of other gene regions as well as broader geographic sampling of specimens will be required to better understand these relationships.

## 3. Billfish population structure

**Blue Marlin:** The blue marlin has a circumtropical distribution, primarily occupying waters with surface temperatures above 24 °C (Nakamura, 1985). Little information is available regarding the spatial and temporal distribution of spawning, although larvae have been collected over broad areas in the Pacific and Atlantic oceans (Nakamura, 1985). Howard and Ueyanagi (1965) reported on spawning of blue marlin and other istiophorids throughout the Pacific Ocean, and several studies have provided insights into the temporal occurrence of blue marlin larvae at specific locations including the Great Barrier Reef, Australia (Leis et al., 1987), Hawaii (Hyde et al., 2005), Exuma Sound, Bahamas (Serafy et al., 2003), Bermuda (Luckhurst et al., 2006), and the northern Gulf of Mexico (Rooker et al., 2012). Conventional tagging studies demonstrate that blue marlin are capable of very high dispersal. Trans-oceanic and trans-equatorial movements have been documented within the Pacific and Atlantic oceans, and two tag recoveries have indicated movements between oceans (Ortiz et al., 2003). Analysis of minimum travel distance versus time at large revealed no apparent cyclical annual movements or site fidelity. Recently, Kraus et al. (2011) reported relatively restricted movements of blue marlin in the Gulf of Mexico based on results from pop-up satellite archival tags. Mean displacement in this study (588 km) was consistent with the results of conventional tagging studies (757 km; Orbesen et al., 2008), however, most of the observed movement involved seasonal north-south displacement. Fish tagged in the western Gulf of Mexico moved from the shelf edge off Texas and adjacent offshore waters in the summer to the shelf edge and adjacent offshore area at the U.S.–Mexico border during spring and fall, and were found in the central region of the Bay of Campeche during the winter months. This suggests the possibility that connectivity between the Gulf of Mexico and the rest of the North Atlantic Ocean may be limited. This is corroborated by the results of conventional tagging

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