A GENETIC PERSPECTIVE ON THE STOCK STRUCTURES OF BLUE MARLIN AND WHITE MARLIN IN THE ATLANTIC OCEAN

J.E. Graves[1,2] and J.R. McDowell[1]

SUMMARY

Investigations of the stock structures of blue marlin (Makaira nigricans) *and white marlin* (Tetrapturus albidus) *within the Atlantic Ocean using analyses of mitochondrial (mt) DNA, single copy nuclear (scn) DNA, and microsatellite DNA are summarized. The levels of variation revealed by the different molecular methodologies varied between species and across molecular markers. In general, variation was very high for both mtDNA and the microsatellite loci. ScnDNA loci were less variable, but sufficiently polymorphic for analyses of population structure. With one exception, analyses of samples from the same location taken in different years did not reveal significant heterogeneity for any of the molecular markers, and allowed us to pool temporal samples, thereby increasing the power of subsequent analyses of spatial heterogeneity. Significant heterogeneity in the distribution of allelic variants among Atlantic sampling locations of either species was not detected for any of the molecular markers. Analysis of molecular variance indicated that among-location variation was negligible within the Atlantic and that essentially all of the variance was maintained within samples. Inclusion of Pacific sampling locations for blue marlin resulted in a significant between-ocean variance component. We were not able to reject the null hypothesis of a common Atlantic-wide genetic stock for either blue marlin or white marlin based on the results of any molecular marker. The genetic data are consistent with the natural history of both species—their continuous distribution across the tropics, broad spawning times and areas, and high vagility as adults—and support the concept that blue marlin and white marlin both comprise single, Atlantic-wide stocks.*

RESUMEN

Se resumen las investigaciones de las estructuras de stock de la aguja azul (Makaira nigricans) *y la aguja blanca* (Tetrapturus albidus) *en el Océano Atlántico utilizando análisis de ADN mitocondrial (mt), copias únicas de ADN nuclear (Scn) y ADN microsatelital. Los niveles de variación revelados por las diferentes metodologías moleculares variaban entre las especies y a través de los marcadores moleculares. En general, las variación era muy alta para el ADNmt y los loci microsatelitales. Los loci de ADN scn eran menos variables, pero lo suficientemente polimórficos para los análisis de estructura de población. Con una excepción, los análisis de muestras del mismo lugar tomadas en años diferentes no revelaron heterogeneidad significativa para ninguno de los marcadores moleculares y nos permitieron reunir muestras temporales, incrementando así la fuerza de análisis posteriores de heterogeneidad espacial. No se detectó para ningún marcador molecular una heterogeneidad significativa en la distribución de variantes alélicas entre los lugares de muestreo del Atlántico de cualquier especie. El análisis de la varianza molecular indicaba que la variación entre lugares era insignificante en el Atlántico y que básicamente, toda la varianza se mantenía dentro de las muestras. La inclusión de lugares de muestreo del Pacífico para la aguja azul tuvo como resultado un componente significativo de varianza entre océanos. Basándonos en los resultados de cualquier marcador molecular, no pudimos rechazar la hipótesis nula de un stock genético común a todo el Atlántico para la aguja azul ni para la aguja blanca. Los datos genéticos son consecuentes con la historia natural de ambas especies -su distribución continua entre los trópicos, amplias temporadas y zonas de desove, y una gran libertad de movimiento como adultos- y respaldan el concepto de que la aguja azul y la aguja blanca comprenden stocks únicos y de todo el Atlántico.*

[1] The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062, US.
[2] e-mail: graves@vims.edu

RÉSUMÉ

Le présent document récapitule les recherches sur la structure des stocks de makaire bleu (Makaira nigricans) *et de makaire blanc* (Tetrapturus albidus) *dans l'Atlantique au moyen de l'analyse de l'ADN mitochondrial (mt), de l'ADN nucleaire à copie simple (SCN) et de l'ADN microsatellitaire. Le niveau de variation révélé par les diverses méthodes moléculaires variait d'une espèce à l'autre et entre les différents marqueurs moléculaires. En général, la variation était très élevée pour l'ADNmt comme pour les loci micro-satellitaires. Quelques loci d'ADNscn étaient moins variables, mais suffisamment polymorphiques pour l'analyse de la structure de la population. A une exception près, l'analyse d'échantillons d'un même endroit prélevés pendant des années différentes n'a révélé d'hétérogénéité significative pour aucun des marqueurs moléculaires, et nous a permis de regrouper les échantillons temporels et d'accroître ainsi la puissance des analyses ultérieures de l'hétérogénéité spatiale. On n'a détecté d'hétérogénéité significative de la distribution des variantes des allèles entre les lieux d'échantillonnage des deux espèces dans l'Atlantique pour aucun des marqueurs moléculaires. L'analyse de la variance moléculaire a indiqué que la variation inter-localisation était négligeable dans l'Atlantique, et qu'essentiellement l'ensemble de la variance se maintenait essentiellement à l'intérieur des échantillons. Le fait d'inclure les lieux d'échantillonnage du Pacifique pour le makaire bleu a donné une composante significative de variance inter-océanique. Nous n'avons pas été en mesure de rejeter l'hypothèse nulle d'un stock génétique commun dans l'ensemble de l'Atlantique, ni pour le makaire bleu, ni pour le makaire blanc, d'après les résultats des marqueurs moléculaires. Les données génétiques sont cohérentes avec l'histoire naturelle de ces deux espèces — leur distribution continue dans les tropiques, leurs zones et époques de frai étendues, et leur forte vagilité en tant qu'adultes— et étayent la notion que le makaire bleu et le makaire blanc constituent tous deux des stocks uniques dans l'ensemble de l'Atlantique.*

KEYWORDS

Stock identification, Fish stocks, Genetics, DNA, Alleles, Population characteristics

INTRODUCTION

The stock structure of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) within the Atlantic Ocean is not well known. Prior to 1996, the Standing Committee on Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) recognized distinct northern and southern stocks of blue marlin and white marlin within the Atlantic Ocean, separated at 5° N. latitude (ICCAT 1997). The original line of demarcation between northern and southern stocks was primarily one of convenience. In the 1970s the international pelagic longline fishery had little effort in this region in the Atlantic Ocean, and it was practical to consider billfish impacted by the northern and southern fisheries as distinct management units.

During the last assessment of blue marlin and white marlin in 1996, the ICCAT SCRS considered two different stock structure scenarios for blue marlin and white marlin in the Atlantic Ocean: (1) northern and southern stocks separated at 5° N, and (2) an Atlantic-wide stock. Based on the continuous distribution of both species across the 5° N boundary throughout the year, tag recapture information demonstrating trans-Atlantic and trans-equatorial movements, and a lack of genetic divergence between samples from the northern and southern hemispheres, the workshop participants felt that the available data were most consistent with the total Atlantic stock hypothesis for both species (ICCAT 1997).

At the time of the 1996 assessment, genetic investigations of blue marlin and white marlin consisted of restriction fragment length polymorphism (RFLP) analysis of whole molecule mitochondrial (mt) DNA (Graves and McDowell 1995). Since that time genetic analyses using a variety of novel, high-resolution molecular techniques have been used to survey samples of both species. For blue marlin these include investigations of stock structure based on analyses of single copy nuclear (scn) DNA loci (Buonaccorsi *et al*. 1999; Graves and McDowell 1999), microsatellite DNA loci (Buonaccorsi *et al*.,

2001), and regions of mtDNA amplified by the polymerase chain reaction (Graves and McDowell 1999). Further studies of white marlin stock structure have included analyses of mtDNA and microsatellite DNA (McDowell *et al*., submitted).

This paper provides an overview of existing genetic analyses of blue marlin and white marlin stock structure within the Atlantic Ocean to better define the appropriate units for the 2000 SCRS stock assessment.

MATERIALS AND METHODS

Sample locations, dates, and sizes are presented in Tables 1 and 2 for blue marlin and white marlin, respectively. Tissue samples consisted of either frozen heart tissue or muscle tissue preserved in tissue storage buffer (Seutin *et al*. 1991) at room temperature. Blue marlin samples were screened for variation within the whole mtDNA molecule, the mtDNA cytochrome *b* gene region, five anonymous scnDNA loci, one nuclear intron region, and five microsatellite loci. White marlin samples were surveyed for variation within the whole mtDNA molecule and four microsatellite loci. Protocols for RFLP analysis of whole molecule mtDNA are reported in Graves and McDowell (1995) and Buonaccorsi *et al*. (1999). Techniques for amplification and analysis of the blue marlin mtDNA cytochrome *b* gene region are described in Graves and McDowell (1999). Protocols for the development and application of five anonymous scnDNA loci are presented in Buonaccorsi *et al*. (1999). Procedures for the analysis of the ribosomal protein 2 gene intron (RP2) in blue marlin are presented in Graves and McDowell (1999). Five tetranucleotide repeat microsatellite loci developed specifically for istiophorid billfishes (Buonaccorsi and Graves 2000) were used to screen blue marlin samples as described in Graves and McDowell (1999). Four of these microsatellite loci were used to survey variation within white marlin samples as indicated in McDowell *et al*. (submitted).

Data Analysis

Detailed descriptions of analytical methods are provided in the above referenced papers. For the purposes of this review, levels of population structuring were evaluated with analyses of heterogeneity and analyses of molecular variation (AMOVA). For mtDNA data, temporal and spatial heterogeneity were evaluated with Monte Carlo simulations of chi-square values as described in Roff and Bentzen (1989) using the computer program REAP (McElroy *et al*. 1991). A hierarchical AMOVA (Excoffier *et al*. 1992) was conducted to partition variance among individuals within samples, among temporal replicates of samples taken in different years from the same location, among locations within the Atlantic Ocean, and for some blue marlin analyses, between Atlantic and Pacific Ocean samples.

The conformance of genotypic distributions of the various nuclear loci (scnDNA and microsatellites) to Hardy-Weinberg expectations was demonstrated in the original manuscripts. Here we present analyses of heterogeneity and AMOVA described in Excoffier *et al*. (1992) implemented by the computer program Arlequin v. 1.1 (Schneider *et al*. 1997). Microsatellite allele data were input both with and without allele relatedness (r and q, respectively) for AMOVA.

RESULTS

Blue marlin

Whole-molecule mtDNA. RFLP analysis of whole-molecule mtDNA of 351 blue marlin from the Atlantic and Pacific Oceans resulted in 127 composite haplotypes (Buonaccorsi *et al*. 2001). Variation was high in all samples, with an overall nucleon diversity of h=0.86. Both nucleon diversity and mean nucleotide sequence diversity were significantly higher in Atlantic samples, due primarily to the presence of a divergent group of haplotypes in approximately 40% of Atlantic blue marlin. Analysis of heterogeneity among temporal samples from Jamaica (6 years), the U.S. mid-Atlantic coast (6 years),

Hawaii (5 years) and Mexico (2 years) revealed one significant result (Hawaii), primarily due to frequencies of a single sample (1994). Results of an AMOVA indicated that the vast majority of variance resided within samples. Temporal variation and variation among samples within an ocean were negligible. However, differences between Atlantic and Pacific Ocean samples were significant. Approximately 22% of restriction site variance was attributable to inter-ocean divergence when relationships among alleles were considered (F), and 3% when allele relationships were not included (q) in the analysis.

Cytochrome b. The mtDNA cytochrome *b* gene region of 455 Atlantic blue marlin was surveyed with 3 restriction endonucleases. Eleven haplotypes were revealed resulting in a haplotype diversity of *h*=0.56 and a nucleotide diversity of p=0.012. Temporal analysis of six robust collectionss from Jamaica (n=266) revealed no significant heterogeneity among samples taken in the same location in different years (p=0.98), and temporal collections at a location were pooled for analyses of spatial heterogeneity. Based on chi-squared randomizations, the observed distribution of haplotypes among geographic locations was not significantly heterogeneous (p=0.56).

ScnDNA. Buonaccorsi *et al*. (1999) surveyed samples of blue marlin from the U.S. mid-Atlantic coast over two years (n=23) and Port Antonio, Jamaica over five years (n=214) with four anonymous scnDNA loci. The Atlantic samples were also compared with 220 individuals collected from Hawaii, Mexico, and Australia in the Pacific Ocean. Diversity of the scnDNA loci was not great, with most systems exhibiting two alleles, one of which occurred at a frequency greater than 0.8 in all collections. AMOVA results indicated no significant partitioning of variation among years at a location. More than 90% of the variance was maintained within samples for each locus. The contribution of differences among locations within the Atlantic and Pacific Oceans was not significantly different from 0; however, differences between samples from different oceans accounted for an average of 8.5% of the total variance.

Microsatellite DNA. Samples of blue marlin from the Atlantic Ocean exhibited very high levels of variation at five tetranucleotide microsatellite DNA loci. The number of alleles per locus varied from 22 to 42, and overall heterozygosities from 0.90 to 0.96 (Table 3). The distributions of alleles among samples from the same location taken in different years were not significantly heterogeneous. Similarly, the distributions of alleles among geographically distant collection locations within the Atlantic Ocean were not significantly heterogeneous. AMOVA indicated that essentially all of the variance was attributed to individuals within samples. Differences among collection locations accounted for up to 0.102% of the total variance for the different microsatellite loci (Table 3).

White marlin

Whole-molecule mtDNA. McDowell *et al*. (submitted) analyzed the whole mtDNA molecule of 236 white marlin with 12 restriction endonucleases revealing 43 composite haplotypes. The temporal stability of haplotype distributions was evaluated among collections taken over several years at three locations: the U.S. mid-Atlantic coast (4 years, n=74), Caribbean (2 years, n=40), and southern Brazil (3 years, n=76). No significant heterogeneity was found among temporal samples at any of the locations (p=0.77 - 0.98) and they were subsequently pooled for analyses of spatial heterogeneity.

Pooling of temporal samples resulted in four collections with 36 or more individuals each: the U.S. (74), Caribbean (40), Brazil (76) and Morocco (36). Six of seven haplotypes represented by four or more individuals in the pooled sample were present in all four geographic locations. The distribution of haplotypes among geographic samples was not significantly heterogeneous (p=0.429).

Population subdivision of white marlin was also evaluated using an AMOVA with haplotypes grouped by individual, temporal collection, and geographic location. When haplotypic frequencies and relatedness data (restriction site gains and losses among haplotypes) were input the among-location component of variance was not significantly different from 0. However, when haplotypic data were entered without

haplotype relatedness considered, the among-location component of variance was small, but signficantly different from 0 (2.73%). This result was primarily due to the absence of one haplotype from the Caribbean collections that occurred in the U.S. sample at 18%, Brazil at 11%, and Morocco at 3%.

Microsatellite DNA. White marlin were screened for variation at four of the five microsatellite loci surveyed in blue marlin. Variation at these loci was high in white marlin, although not as high as in blue marlin. The number of alleles per locus ranged from 12 to 25, and overall heterozygosities ranged from 0.82 to 0.95 (Table 3). AMOVA demonstrated that differences between temporal collections at a location were not significantly different from 0. The vast majority of variance was attributed to individuals within samples, and variance resulting from among-location differences was negligible.

DISCUSSION

Molecular genetic analyses provide a means to investigate the stock structure of highly migratory species. Significant differences in allele frequencies between samples may be indicative of stock boundaries, although caution should be applied in the interpretation of genetic data. The observation of genetic heterogeneity among samples alone does not necessarily demonstrate stock structure (Waples 1998). Sampling error, sex- or age-related differences in allele frequencies, or a high variance in reproductive success (recruitment) can result in significant but ephemeral heterogeneity that could mistakenly be interpreted as stock structure (Gold *et al*. 1997).

Alternately, the observation of a lack of significant allele frequency differences among collection locations does not necessarily signify that population structuring does not exist. Gene flow on the order of a few individuals per generation may be sufficient to prevent the accumulation of significant genetic differences among locations (Waples 1998). What might amount to trivial emigration for a fisheries manager, may be sufficient to maintain genetic homogeneity.

The molecular techniques used to survey the genetic basis of stock structure within Atlantic blue marlin and white marlin revealed considerable variability. Analyses of whole molecule mtDNA, the mtDNA cytochrome *b* gene region, and nuclear microsatellite loci all demonstrated extremely high levels of variation. In general, comparable analyses of whole molecule mtDNA and nuclear microsatellite DNA loci demonstrated higher levels of variation within blue marlin than white marlin. The scnDNA loci surveyed in blue marlin were not as variable as other molecular markers, but were sufficiently polymorphic for analyses of stock structure.

Samples of blue marlin and white marlin were collected at several locations over a period of two or more years. With the exception of one locus at one Pacific Ocean location for blue marlin, no significant heterogeneity was observed among temporal samples from the same location for either species. This allowed samples collected in different years at a location to be pooled, thereby increasing effective sample size and the power of subsequent analyses of spatial heterogeneity.

No significant spatial heterogeneity was revealed among sampling locations of blue marlin or white marlin within the Atlantic Ocean by any of the molecular markers employed in the analyses. Similarly, in the AMOVA for each marker, the magnitude of variance among sampling locations within the Atlantic Ocean was negligible. For both Atlantic blue marlin and white marlin, the null hypothesis that samples originated from a common gene pool was not rejected based on the allelic distribution of any molecular marker. In contrast, blue marlin exhibited highly-significant heterogeneity between Atlantic and Pacific Ocean samples, and a significant fraction of overall variance of each molecular marker was attributed to differences in the distribution of alleles between ocean collections of blue marlin.

The molecular genetic techniques employed in this analysis did not reveal significant heterogeneity among samples of blue marlin or white marlin taken from geographically distant locations within the Atlantic Ocean; however, similar techniques have revealed significant within-ocean population structur-

ing of other highly migratory species. RFLP analysis of whole molecule mtDNA demonstrated significant heterogeneity among samples of striped marlin taken from widely separated locations within the Pacific Ocean (Graves and McDowell 1994). Similarly, RFLP analysis of mtDNA and nuclear gene regions has been used to demonstrate spatial heterogeneity among Atlantic swordfish (Chow and Takeyama 2000) and albacore (Chow and Ushiama 1995). RFLP analysis of whole molecule mtDNA or amplified mtDNA gene regions has been used to reveal significant population structuring between ocean populations of several highly migratory species, including albacore, bluefin tuna, bigeye tuna, swordfish, blue marlin and white marlin (reviewed in Graves 1998).

The results of investigations of the stock structure of blue marlin and white marlin employing a variety of molecular markers support the hypothesis that both species comprise single genetic stocks within the Atlantic Ocean. The genetic results are consistent with other aspects of the biology of these highly migratory fishes. Both blue marlin and white marlin are continuously distributed across the 5° N latitude throughout the year, and individuals of each species are known to undertake extensive movements, including trans-Atlantic and trans-equatorial migrations (reviewed in ICCAT 1997). Thus, the potential for gene flow exists, and the molecular data indicate that sufficient exchange occurs to prevent the accumulation of significant genetic divergence.

The existence of single stocks of blue marlin and white marlin within the Atlantic Ocean does not imply that each species comprises a panmictic population. Tagging data clearly demonstrate that an individual blue marlin or white marlin in the northwest Atlantic are more likely to interact with conspecifics from the northwest Atlantic than individuals from the southeast Atlantic. This implies some degree of isolation-by-distance. Consequently, it is likely that regional conditions favoring recruitment could result in local abundances, and increased fishing effort in areas could result in regional overfishing. The time course over which such increases or decreases in abundance would persist is not known. To estimate exchange rates of these highly migratory species will require non-genetic technologies such as conventional or satellite tagging.

In conclusion, it is appropriate to manage blue marlin and white marlin as single Atlantic-wide stocks. Both species are distributed continuously throughout the subtropical and tropical waters of the Atlantic Ocean, undertake extensive movements, spawn over a broad region, and demonstrate genetic continuity throughout the ocean basin - any line subdividing either species within the Atlantic would be arbitrary and inconsistent with the biological data.

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Table 1. Collection information for blue marlin samples from the Atlantic Ocean. Included are sample location, date, size, and the number of individuals assayed by the various molecular genetic techniques. Location abbreviations are as follows: JAM = Port Antonio, Jamaica; US = Cape May, New Jersey, USA; BAH = Bahamas; BRA = Santos, Brazil; and GHA = Teme, Ghana. Abbreviations of molecular genetic techniques are as follows: WHMOL = RFLP analysis of whole molecule mtDNA; CYTB = RFLP analysis of an amplified gene region including cytochrome *b* gene; Mn01, Mn10, Mn08, Mn60, and Mn90 = analysis of five distinct tetranucleotide repeat microsatellite loci; and RP2 = RFLP analysis of an intron of the RP2 gene.

Location	Molecular Genetic Technique							
	WHMOL	CYTB	Mn01	Mn10	Mn08	Mn60	Mn90	RP2
JAM91	28	53	48	51	47	48	48	57
JAM92	54	58	51	52	52	54	52	56
JAM93	18	41	41	41	39	41	41	38
JAM94	43	47	46	52	45	46	45	34
JAM95	21	24	24	24	24	24	23	24
JAM97	0	43	29	35	27	0	0	41
US92	12	12	12	11	12	13	13	11
US93	5	7	5	6	5	6	3	0
US94	9	13	14	14	13	11	11	13
US95	0	13	0	13	0	0	0	13
US96	0	12	0	0	0	0	0	0
US98	0	5	5	7	4	0	0	7
BAH97	0	5	4	5	2	0	0	5
BAH 98	0	23	21	22	21	0	0	21
BRA92	0	9	9	9	9	9	9	0
BRA98	0	39	37	38	37	0	0	39
BRA99	0	10	2	9	5	0	0	13
GHA98	0	49	28	39	46	0	0	36
TOTAL	190	455	376	428	388	252	245	408

Table 2. Collection information for white marlin samples. Included are sample location, date, size, and the number of individuals assayed by the various molecular genetic techniques. Location abbreviations are as follows: USA = Cape May, New Jersey, USA; BRA = Santos, Brazil; DOM = Dominican Republic; MOR = Casablanca, Morocco; and VEN = Cumana, Venezuela. Abbreviations of molecular genetic techniques are as follows: WHMOL = RFLP analysis of whole molecule mtDNA; Mn01, Mn10, Mn08, and Mn60 = analysis of four distinct tetranucleotide repeat microsatellite loci.

Location	Molecular Genetic Technique				
	WHMOL	Mn01	Mn08	Mn10	Mn60
BRA92	28	0	0	0	0
BRA93	35	13	9	13	14
BRA95	13	14	18	16	11
USA92	15	14	14	16	15
USA93	18	7	16	16	17
USA94	27	17	22	23	8
USA95	14	13	16	12	16
DOM92	18	13	12	0	13
MOR95	22	27	34	31	36
VEN96	36	24	25	24	19
TOTAL	226	145	166	151	141

Table 3. Analysis of five tetranucleotide repeat microsatellite DNA loci within Atlantic blue marlin and white marlin. Included are the locus name (Locus), number of alleles (A), overall heterozygosity (H), and percentage of the total variance due to among-location (Atlantic) structuring (%VAR).

	BLUE MARLIN			WHITE MARLIN		
Locus	A	H	%VAR	A	H	%VAR
Mn01	24	0.93	-0.107	12	0.82	0.340
Mn08	42	0.96	-0.220	25	0.95	-0.350
Mn10	22	0.90	0.082	15	0.83	-0.060
Mn60	22	0.92	-0.005	18	0.90	0.900
Mn90	28	0.94	0.102			