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An Exploratory Analysis to Identify Reproductive Strategies of Billfishes

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ABSTRACT

This contribution is aimed to the identification of reproductive patterns of billfishes, which is in turn a key issue supporting management and conservation policies. Information reported in the literature on features of reproductive processes of billfishes was examined with a Principal Components Analysis (PCA) to identify groups of species with similar reproductive strategies. PCA was applied based in a correlation matrix and the significances ($p<0.05$) of the factors and loadings of the variables were used as criteria for the identification of reproductive patterns. In general, four groups were found. The first group consists of *Tetrapturus albidus* and *T. audax*, which are characterised by rapid growth, an early age at first maturity with respect to maximum age (T/Tmax) and high values of reproductive variables (e.g., Spawning Duration (Sd), Spawning Frequency (Sf), Annual Fecundity (AF) and Relative Fecundity (RF). A second group consists of *T. belone*, *T. georgii* and *T. pfluegeri*, which present rapid growth, high Tm/Tmax ratios and Batch Fecundity (BF) values and low Sd values. Another group consists of the genera *Makaira* and *Xiphias*, which present low Lm/Lmax ratios and high values for AF, RF, Sf and BF. The last group consists of species of the genus *Istiophorus*, which present the lowest AF values and the highest RF and BF values. In billfishes, the reproductive pattern is strongly influenced by the growth process and the age at which a species reaches sexual maturity relative to its maximum age. The observed differences in reproductive variables result from adaptive mechanisms that allow species greater reproductive success in the epipelagic environment.

Key words: Billfishes, reproductive patterns, migratory fish, epipeligc environment

INTRODUCTION

Among the important parameters in reproductive biology are the breeding season and area, the age at maturity, the age at first reproduction and fecundity (Jakobsen *et al*., 2009). One of the most important aspects for the sustainable use and management of living marine resources is the maintenance of vital rates that will produce the highest levels of resilience. The vital rates are of great importance to reproductive success, which depends on both fishing yields and population maintenance. In this context, understanding the parameters that characterise reproductive processes can help managers determine, for example, the effects of fishing on the renewal potential of stocks (Mace, 1993; Murawski *et al*., 2001). Investigating these parameters has allowed the characterisation of reproductive strategies, which in turn correspond to species' adaptations to environmental conditions (Maury and Lehodey, 2005).

Comparative studies of these parameters have been widely recognised; however, for some fish, such as billfishes, studying reproductive parameters is a complex process because the fish migrate and there is insufficient knowledge of breeding areas (Richardson *et al.*, 2009a, b). The management of these species is challenging partly because of their migratory nature, which hinders the study of their life histories, habitat requirements and stock sizes (ICCAT, 2006) and causes the fishes to cross jurisdictional boundaries.

Studies on reproductive processes of billfishes have mainly focused on two or three species (e.g., *Xhiphiias gladius* and*Tetrapturus audax*), although most species are targeted for commercial and recreational fisheries around the world (Fromentin and Fonteneau, 2001; Brinson *et al.*, 2009). Moreover, most knowledge of reproductive aspects is limited to certain regions and time periods (ICCAT, 2004) and little is known on a global scale.

In general, it is recognised that distributional differences (tropical or temperate) correspond to differences in characteristics of these species and their responses to fishing pressure (Pauly, 1998; Fromentin and Fonteneau, 2001; Boyce *et al.*, 2008). We hypothesis that different reproductive strategies among billfishes can be identified by examining combinations of reproductive characteristics with their variations. Thus, the aim of this study was to synthesise available information on reproduction of these species to identify patterns in the reproductive process.

MATERIALS AND METHODS

We collected information on reproductive life histories of species in the fish families Xiphiidae and Istiophoridae using literature from databases, such as ASFA (Aquatic Sciences and Fisheries Abstracts), EBSCOhost (http://www.ebscohost.com/), FishBase (www.FishBase.org.) and grey literature (thesis dissertations, technical reports). Key parameters that characterise the reproductive process are listed below. In this list, age is measured in years and length is defined as the Lower Jaw-Fork Length (LJFL) and is measured in centimetres unless otherwise specified.

- Length (Lmax) and maximum age (Tmax)
- Length (Lm) and age (Tm) at first maturity (at which 50% of the individuals are mature and able to reproduce)
- Duration of the spawning period (Sd) (the number of months per year during which spawning occurs, measured in days)
- Spawning frequency (Sf) (number of spawns per month, measured in days)
- Relative Fecundity (RF) (number ova/grams of body weight)
- Batch Fecundity (BF) (number of ova)
- Annual Fecundity (AF) (i.e., the product of batch fecundity, spawning frequency and the duration of the spawning season)

Because some species are sexually dimorphic (e.g., *X. gladius* and *Makaira* spp.), certain features were reported separately for each sex in the literature; in these cases we used the data on females. Because most researchers did not report all of the parameters listed above, we also considered additional information to estimate missing data. For example, we used the parameters of the Von Bertalanffy growth equation (Von-Bertalanffy, 1938), K (y^{-1}), L_8 (cm) and t_0 (y^{-1}), or estimate some of them when needed (Pauly, 1980; Froese and Binohlan, 2000; Froese and Pauly, 2000). Also, in some cases, length and maximum age were used to estimate the length and age at first maturity (Froese and Binohlan, 2000). Other empirical equations were also used to calculate total length, total weight, eye-fork length and gutted weight (Wares and Sakawa, 1974; Prince, 1990; Prager *et al*., 1995; IOTC, 2005).

Statistical analysis: We used a Principal Component Analysis (PCA) based on a correlation matrix to analyse the reproductive data for different species. The statistical significance of the components and the contribution of each variable in each component (i.e., loading) were computed following a procedure that is based on the rotation of the normalised variance method (Kaiser, 1960). In our case, loading values ≥ 0.7 were considered significant.

RESULTS

The life history parameters considered for our analysis are shown in Table 1. From the eleven species analysed, only three (*X. gladius*, *T. audax* and *I. platypterus)* were described by all of the reproductive variables, while values for some variables were not available for *Tetraturus belone*, *T. pfluegeri*, *T. georgii* and *T. angustirostris*. Other species account for some variables.

We did a preliminary analysis to explore how variables were related and to identify whether a significant correlation could bias the results of the PCA. Table 2 shows the significant correlations ($p<0.05$); correlations between Wm and Lmax, Wmax, Tmax and BF, as well as between BF and Lmax, Wmax, Tmax and Wm showed evidence some autocorrelation through Wm. Thus, this

Table 1: Life history parameters for billfish species related to reproductive process. Estimates were based on empirical equations appears in bold letters

Species	Lmax (cm)	Wmax (kg)	Tmaxyr	Lm (cm)	Wm (kg)	Tm (tr)	K (year^{-1})	Sd (month)	Bf * (ova)	Af * (ova)	Rf (ova/G)	Sf (days)	Ref
Istiophorus albicans	259	53	8	158.3	17.5	2.8	0.375	6.1	1.6	12.15	36		a
Istiophorus platypterus	260	60	12	185.6	28	5	0.25	5.8	2.15	680.13	50	3.1	b
Makaira indica	368	525	20	220.6	85	3.5	0.09	3		145.5			c
Makaira nigricans	457	541	17	213	108	4	0.12	5	8.51	225.06	55.5	5.4	d
Tetrapturus albidus	210	67.1	9	156.12	22	1.5	0.67	4	0.59	23.25	17.1	1.5	e
Tetrapturus audax	283	106	11	173	60	1.9	0.59	3	3.1	67	29.7	2.2	f
Tetrapturus angustirostris	222	52	6	132		1.9	0.5						g
Tetrapturus belone	195	36	5	150		2	0.6	6					h
Tetrapturus georgii	200	24	5	155		2	0.6	5	0.32				i
Tetrapturus pfluegeri	194	45	5	150	19	2	0.6	5.3	0.41				j
Xiphias gladius	351	506	16	166	75	4.6	0.14	4.5	6.32	146.6	36.7	3.5	k

*millions. Lmax: Maximum length (cm); Wmax: Maximum weight (g); Tmax: Maximum age (year); Lm: Length (cm) at first maturity; Wm: Weight at first maturity; Tm: Age (year) at first maturity; K (y^{-1}): Von Bertalanffy growth coefficient; Sd: Spawning duration (month); Bf: Batch fecundity(ova/spawning); Af: Annual fecundity (ova); Rf: Relative fecundity (ova/g); Sf: Spawinig frequency (days). Ref: References as follows: (a): Arocha and Marcano (2006), Bumguardner and Anderson (2008), De Sylva and Breder (1997), Garcia de los Salmones *et al*. (1989), Jolley (1977), N´Da and Soro (2009), Souza *et al*. (1994); (b): Eldridge and Wares (1974), Hernandez-Herrera *et al*. (2000), Hernandez-Herrera and Ramirez-Rodriguez (1998), Hoolihan (2006), Chiang *et al*. (2006a,b); (c): Pepperell (2000), Speare (2003), Speare and Williams (1994); Sun *et al*. (2007), (d): Brown-Peterson *et al*. (2008), Bumguardner and Anderson (2008), De Sylva and Breder (1997), www.fishbase.org, Luckhurst *et al*. (2006), Molony (2008), Pepperell (2000), Shimose *et al*. (2009), Sun *et al*. (2009), (e): Arocha and Barrios (2009), Baglin (1977), Garcia de los Salmones *et al*. (1989), Oliveira *et al*. (2006); Souza *et al*. (1994), (f): Kopf *et al*. (2009), Van der Elst (1981), (g): www.fishbase.org, Molony (2008); (h): Arocha and Ortiz (2006b), http://www.efsa.co.uk/record/spearfishmed.htm, (I); Arocha and Ortiz (2006a), Nakamura (1985), (j): Arocha and Ortiz (2006a), De Sylva and Breder (1997), www.fishbase.org, Souza *et al*. (1994), (k) Arocha and Lee (1995), Cavallaro *et al*. (1991), De la Serna *et al*. (1992), De Martini *et al*. (2000), Garcia and Mejuco (1988), Hazin *et al*. (2002), Poisson and Fauvel (2009), Taylor and Murphy (1992), Young *et al*. (2003)

Table 2: Correlation coefficients between variables considered for PCA

	Lmax	Wmax	Tmax	Lm	Wm*	Tm	BF	AF	RF	SD	FS	K
Lmax	1.00											
Wmax	**0.91**	1.00										
Tmax	**0.94**	**0.94**	1.00									
Lm	0.78	0.48	0.64	1.00								
Wm*	**0.97**	**0.89**	**0.88**	0.67	1.00							
Tm	0.48	0.48	0.70	0.48	0.31	1.00						
BF	**0.99**	**0.95**	**0.97**	0.68	**0.97**	0.51	1.00					
AF	-0.02	-0.18	0.12	0.41	-0.21	0.74	-0.06	1.00				
RF	0.72	0.49	0.73	**0.89**	0.56	0.81	0.66	0.68	1.00			
SD	0.24	0.20	0.40	0.49	0.01	0.83	0.22	0.84	0.72	1.00		
FS	**0.95**	0.82	**0.92**	**0.88**	0.85	0.66	**0.92**	0.28	**0.88**	0.53	1.00	
K	-0.77	-0.77	**-0.92**	-0.63	-0.64	**-0.92**	-0.80	-0.48	-0.85	-0.70	**-0.88**	1.00

Significant correlations ($p<0.05$) are in bold. Lmax: Maximum length (cm); Wmax: Maximum weight (g); Tmax: Maximum age (year); Lm: Length (cm) at first maturity; Wm: Weight at first maturity; Tm: Age (year) at first maturity; K (y^{-1}): Von Bertalanffy growth coefficient; Sd: Spawning duration (month); Bf: Batch fecundity (ova/spawning); Af: Annual fecundity (ova); Rf: Relative fecundity (ova/g); Sf: Spawning frequency (days). *Variable not used for the final analysis (see text for explanation)

Table 3: Results of the primary principal components analysis (PCA) of variables associated with reproductive processes of billfishes. PCA# indicates different scenarios of PCA

Variable	PCA1 Factor 1	PCA2 Factor 1	PCA2 Factor 2	PCA3 Factor 1	PCA3 Factor 2	PCA4 Factor 1	PCA4 Factor 2	PCA5 Factor 1	PCA5 Factor 2
Lmax (cm)	**-0.953**	**0.900**	0.298	**0.970**	0.034	**0.969**	0.127	**0.980**	0.139
Wmax (kg)	**-0.915**	**0.857**	0.374	**0.933**	-0.024	**0.964**	-0.014	**0.963**	-0.002
Tmax (year)	**-0.950**	**0.889**	0.431	**0.969**	0.013	**0.948**	0.191	**0.943**	0.281
Lm (cm)	**-0.823**	**0.828**	0.365	**0.825**	0.162	0.69	0.46	0.615	0.548
Tm (tr)	**-0.830**	**0.893**	-0.315	0.681	0.638	0.466	**0.812**	0.416	**0.829**
K ($year^{-1}$)	**0.946**	**-0.987**	0.021	**-0.832**	-0.535	-0.7	-0.64	-0.737	-0.622
Sd (month)	na	**-0.104**	**-0.967**	-0.151	**0.953**	-0.121	**0.819**	0.142	0.925
Bf (ova)	na	na	na	**0.988**	-0.005	**0.995**	0.079	**0.994**	0.099
Af (ova)	na	na	na	na	na	0.028	**0.864**	-0.161	**0.979**
Rf (ova/G)	na	na	na	na	na	0.577	**0.765**	0.588	**0.766**
Sf (days)	na	na	na	na	na	na	na	**0.885**	0.430
Expl.Var (%)	81.79	68.60	22.60	69.80	20.40	52.90	33.40	54.84	36.97

Significant ($p<0.05$) components (factors) and variables within each factor (loadings>0.7) are indicated in bold. Values for some variable are not included in the analysis because there were no data (na = not applicable). Expl.Var. refers to the variance explained by each factor

variable was eliminated from the analysis. Other significant correlations did not show clear evidence of functional relationships or patterns that could be maintained across species. Because there was not enough evidence to eliminate other variables, we made a first approximation of the PCA with all variables except Wm.

Given that a PCA requires complete data sets and that our data set was incomplete for some species, it was not possible to incorporate all of the parameters into a single analysis. Therefore, different species combinations were used to explore the different variables and species. Table 3 shows the combinations and the main results.

Present initial analysis produced two main findings. The variables in the first component, Lmax Wmax, Tmax and, except in two cases, Lm, were consistently significant. Also, species tended to fall into three groups, corresponding to the genus: *Istiophorus*, the complex *Makaira-Xiphias* and a third group called *Tetrapturus1* (which includes species *T. albidus* and *T. audax*). Significant variables resulting from the PCA, in conjunction with the significant correlations in Table 2, suggest covariance or functional relationships between some of the variables. For this reason, the PCA was redefined with the following variables: Lm/Lmax, Wmax, K, Sd, BF, AF, RF and Sf. Lm/Lmax is an index that relates the size at which a fish reaches maturity to the maximum size of the fish; it is an expression that, from a physiological point of view, is equivalent to Tm/Tmax. The species *Tetrapturus angustirostris* was not included in the PCA because of the lack of reproductive data for these parameters.

Results of the five PCA scenarios are shown in Table 4a and b. In general, groups similar to those described above were identified and, when other species of *Tetrapturus* were incorporated into the analysis (scenarios PCA9 and PCA10), they formed a second group we named Tetrapturus2 (Fig. 1).

Table 4a: Results of the principal components analysis (PCA) applied to variables associated with reproductive processes of billfishes. PCA# indicates different applications of PCA

	PCA6	PCA6	PCA7	PCA7	PCA8	PCA8	PCA9	PCA9	PCA10
Variable	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1
Lm/Lmax	**-0.983**	0.082	**-0.970**	0.050	**0.889**	-0.140	**0.955**	-0.082	**0.920**
Wmax (kg)	**0.977**	0.016	**0.972**	0.002	**-0.957**	0.175	**-0.964**	0.081	**-0.966**
K (year^{-1})	**-0.747**	-0.624	**-0.740**	-0.642	**0.879**	0.401	**0.872**	0.444	**0.892**
Sd (month)	0.124	**0.939**	-0.042	**0.822**	**0.081**	**-0.804**	0.056	**-0.993**	0.423
BF (ova)	**0.989**	0.120	**0.979**	0.104	na	na	**-0.986**	0.072	na
AF (ova)	-0.178	**0.967**	-0.080	**0.860**	-0.030	**-0.864**	na	na	na
RF (ova/G)	0.554	**0.783**	0.539	**0.789**	na	na	na	na	na
Sf (days)	**0.855**	0.463	na	na	na	na	na	na	na
Expl.Var (%)	56.772	38.169	52.739	35.177	49.766	32.086	71.493	24.028	68.862

Significant ($p<0.05$) components (factors) and variables within each factor (loadings>0.7) are indicated in bold.Values for some variable are not included in the analysis because there were no data (na = not applicable). Expl.Var. refers to the variance explained by each factor. K: Von Bertalanffy growth coefficient; Sd: Spawning duration; BF: Batch fecundity; AF: Annual fecundity; RF: Relative fecundity; Sf: Spawning frequency

Table 4b: Results of the principal components analysis (PCA) applied to variables associated with reproductive processes of billfishes. PCA# indicates different applications of PCA

	PCA6	PCA6	PCA7	PCA7	PCA8	PCA8	PCA9	PCA9	PCA10
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1
Istiophorus albicans			-0.524	0.103	-0.696	-0.240	0.256	**-1.064**	0.357
Istiophorus platypterus	**1.185**	**1.233**	**-1.034**	**1.443**	-0.607	**-1.975**	0.304	**-1.176**	0.383
Makaira indica	na	na	na	na	**1.061**	0.506	**-1.184**	-0.424	**-1.552**
Makaira nigricans	**0.813**	**-0.867**	**0.939**	**0.711**	**1.117**	-0.248	na	na	**-1.258**
Tetrapturus albidus	**-1.047**	0.423	-0.479	**-1.199**	**-0.961**	**0.891**	0.334	**1.121**	0.227
Tetrapturus audax	**-0.914**	0.392	-0.437	**-0.978**	**-0.918**	**0.958**	0.248	**1.715**	0.032
Tetrapturus belone	na	na	na	na	na	na	na	na	**1.038**
Tetrapturus georgii	na	na	na	na	na	na	**1.049**	-0.115	**1.102**
Tetrapturus pfluegeri	na	na	na	na	na	na	**0.848**	-0.242	**0.916**
Xiphias gladius	-0.038	**-1.181**	**1.535**	-0.080	**1.004**	0.109	**-1.856**	0.186	**-1.246**

Significant ($p<0.05$) components (factors) and species within each factor (loadings>0.7) are indicated in bold. Values for some variable are not included in the analysis because there were no data (na = not applicable). Expl. Var. refers to the variance explained by each factor

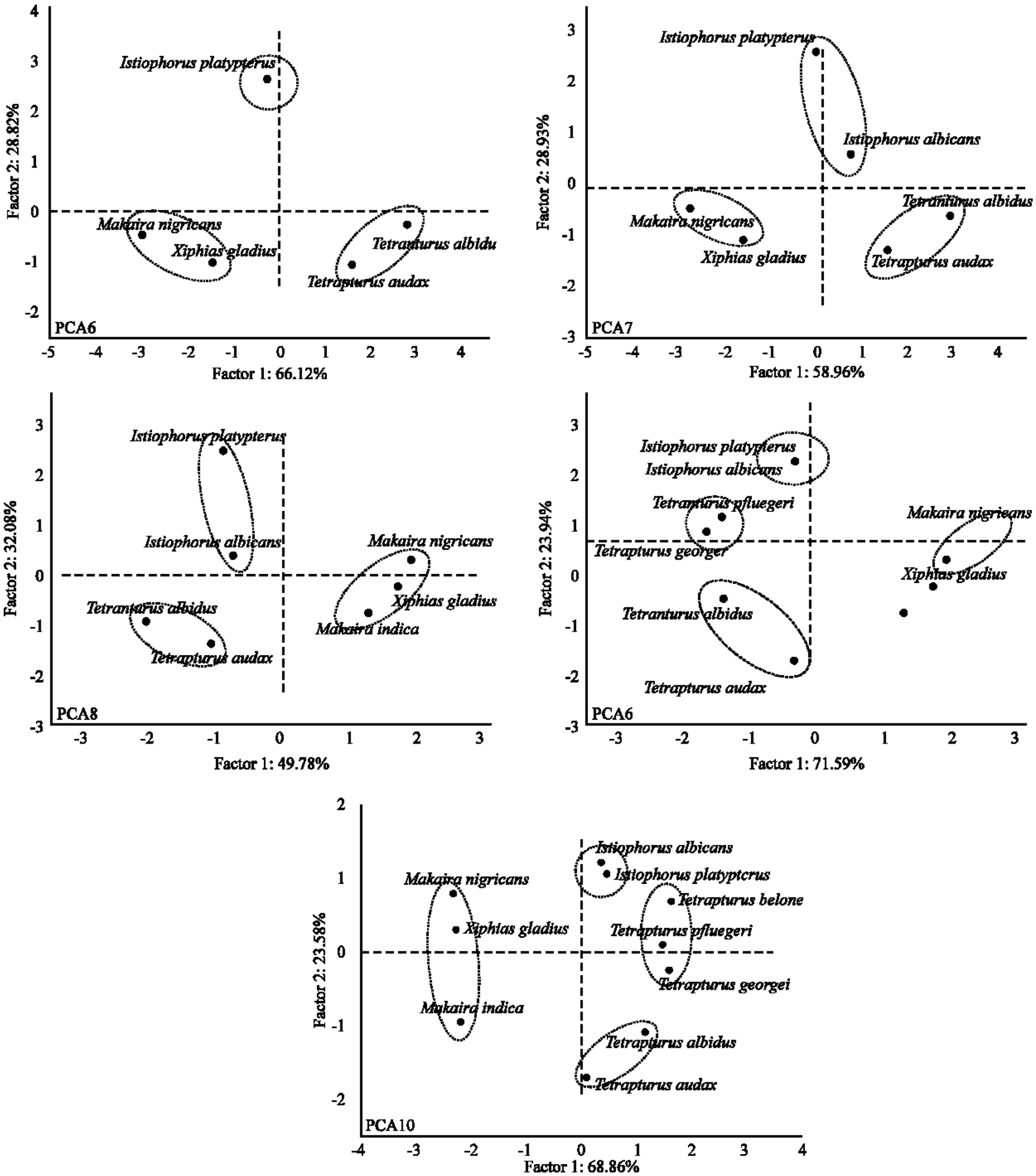

Fig. 1: Graphs of five PCA scenarias

With respect to the significant variables, there are two types: those associated with individual development (i.e., K, Wmax and Lm/Lmax), which were significant in the first component in almost all PCA scenarios and those directly expressing an attribute of the reproductive process. For the latter, two variables represent the number of eggs produced (RF and BF) and three variables represent reproductive rates (Sd, AF, Sf). Except for Sf in the PCA6 scenario, these rates were consistently significant in the second component.

Results from the PCA suggest the presence of four groups with clearly identifiable reproductive characteristics (Fig. 1):

Tetrapturus 1: This group is represented by the species *T. albidus* and *T. audax*. These species are generally associated with the lowest values of the reproductive variables (i.e., Sd, Sf, AF and RF). The low Tm/Tmax ratios (<20%) and the high values of the growth coefficient, K, suggest rapid growth and early maturity.

Tetrapturus 2: This group is represented by the species *T. belone*, *T. georgii* and *T. pfluegeri*. While these species are fast growing, they reach maturity at old ages (Tm/Tmax = 40%). They also are small in size and weight and have a longer spawning duration (Sd) and lower batch fecundity (BF).

Makaira-Xiphias: This group consists of species of the genera *Makaira* and *Xiphias*. Among billfish, the species in this group have the lowest Lm/Lmax ratios (50-60%) and they have relatively low Tm/Tmax ratios; these data suggest that the fish in this group mature at relatively small sizes even when they have a slow growth rate. These species also tend to have a high Spawning Frequency (SF) and the highest values of annual, relative and batch fecundities (AF, RF and BF, respectively).

Istiophorus: This group consists of species of the genus *Istiophorus*, specifically *I. albicans* and *I. platypterus*. They present intermediate values of the growth coefficients and of the Lm/Lmax ratio. However, they have the lowest values of AF and relatively high values of Sd, RF and BF.

DISCUSSION

Females of most billfishes species reach sexual maturity at larger sizes than do males (Nakamura, 1985); this pattern is the only type of "sexual dimorphism" that is non-apparent, although it has been reported that some species, such as *T. pfluegeri*, *T. belone* and *T. angustirostris*, do not show such differences. The first two classified within the group Tetrapturus 2 (the third one was not into the analysis because absence of data).

Most studies reported that spawning duration time is approximately 3 to 6 months and, for some species, such as *I. platypterus* and *I. albicans*, there are two reproductive periods. De Sylva and Breder (1997) indicated that males can reproduce year round. Spawning frequency (Sf) data indicate that billfishes lay eggs between 1.5 to 5.4 days.

M. nigricans has a Sf that ranges from 2.4 to 8.3 days and is therefore the species with the greatest range of Sf values during the breeding season. Also, this species has the highest BF and is the largest in length and weight. Relatively larger females are physiologically capable of maintaining higher reproductive frequencies, so this seems to be related to their energy reserve (Schaefer, 2003). The variability in BF can change from year to year for similarly sized individuals that are of the same species and in the same area (Schaefer, 1998). Some factors, such as food, growth rate and population density, influence this variability (Tamate and Maekawa, 2000; Blanck and Lamouroux, 2006).

By observing the distinctive characteristics of each group (Table 5), it is clear that growth is strongly associated with the reproductive processes of these species. In particular, growth is related to how fast a female reaches sexual maturity and, in this context, growth is associated with the

Table 5: Relationships between variables associated with the reproductive processes of billfishes

Ind. variable	Dep. variable	a	b	r^2	F	p<0.05
K	Tmax	0.810	-0.038	0.760	25.900	0.001
K	Wmax	0.574	-0.001	0.709	19.530	0.002
K	Tm	0.888	-0.165	0.788	29.870	0.001
K	Lmax	1.023	-0.002	0.735	22.140	0.002
K	Lm	1.647	-0.007	0.628	13.510	0.006
K	Lm/Lmax	-0.555	1.457	0.599	11.990	0.009
K	Rf	0.891	-0.014	0.727	10.650	0.031
Lm	Rf	126.535	1.301	0.714	10.070	0.034
Lm/Lmax	Bf	16.525	-20.969	0.850	35.130	0.001
Lmax	Wmax	205.530	0.360	0.840	43.040	0.000
Lmax	Tmax	114.800	14.990	0.820	35.770	0.000
Lmax	Lm	-230.423	2.935	0.712	19.809	0.002
Lmax	Lm/Lmax	709.790	-658.437	0.836	40.690	0.000
Tm/Tmax	Sd	-0.077	0.079	0.731	21.711	0.002
Tmax	Lm/Lmax	33.750	-34.880	0.650	14.540	0.005
Tmax	Lm	-21.229	0.185	0.780	28.570	0.001
Wmax	Tmax	-214.660	38.050	0.820	36.600	0.000
Wmax	Lm/Lmax	1196.900	-1521.300	0.695	18.250	0.003
Wmax	Lm	-963.641	6.713	0.581	11.084	0.010
Wmax	Bf	-22.555	68.802	0.919	68.340	0.000
Lm	Tm	137.850	11.929	0.338	4.090	0.078
Lm	Lm/Lmax	253.959	-123.385	0.354	4.390	0.069
Tm	Rf	0.129	0.085	0.652	7.510	0.052
Tm	Af	2.542	0.004	0.543	5.950	0.059
Tmax	Tm/Tmax	20.232	-31.399	0.374	4.780	0.060

Significance was set at $p<0.05$, with the exception of the last five relationships, which were significant at $p<0.10$ (ind.=independent; dep.=dependent). K (y^{-1}): Von Bertalanffy growth coefficient; Lm: Length (cm) at first maturity; Lmax: Maximum length (cm); Tm: Age (year) at first maturity; Tmax: Maximum age (year); Wmax: Maximum weight (g); Af: Annual fecundity (ova); Rf: Relative fecundity (ova/g); Sd: Spawning duration (dais); Bf: Batch fecundity (ova/spawning). Note that spawning frequency, Sd, was not significantly correlated with any variable. a and b are regression parameters, r^2 is determination coefficient expressing how much variance of dependent variable is explained by independent variable, F corresponded to F test for significance

significant variables Lm and Lmax. Thus, the Relative Fecundity (RF) is significantly correlated with K, Lm and Tm; the Batch Fecundity (BF) is correlated with Wmax and the Lm/Lmax ratio; the Annual Fecundity (AF) is correlated Tm; and the spawning duration (Sd) is correlated with the Tm/Tmax ratio.

Billfish are considered epipelagic species (Block *et al.*, 1992; Boggs, 1992) that occupy high trophic levels >5 when they are adults (Griffiths *et al.*, 2010). Usually, billfishes occupy the same habitat and their distribution often overlap spatially (Campbell and Young, 2008; Shimose *et al.*, 2010; Young *et al.*, 2010). However, each species tolerates different ranges of environmental variation (Nakamura, 1985; Bigelow *et al.*, 1999). Their potential prey may also be similar (Shimose *et al.*, 2010) but may vary between seasons, years, areas and target preys. This variation may reduce competition for food (Young *et al.*, 2010) and thus may be an adaptive strategy that allows billfishes to exploit the same environment (Dagorn *et al.*, 2000).

All billfish species are partial or multiple spawners with asynchronous development of oocytes (De Sylva and Breder, 1997; Hernandez-Herrera *et al.*, 2000; Murua and Saborido-Rey, 2003;

Arocha *et al*., 2005; Kopf *et al*., 2009). Present a pattern with an indeterminate annual fecundity and therefore the breeding season is prolonged, characteristic of species with this reproductive pattern (Brown-Peterson *et al*., 1988). According to Lambert and Ware (1984), partial spawning may be a strategy to release eggs over a long period of time, thus increasing the probability of progeny survival.

According to Murua *et al*. (2003), variation in reproductive characteristics of a species is a function of or a response to, variation in environmental conditions, such as temperature, food availability, habitat and predation intensity; however, the migratory nature of these species allows them to exploit the resources of their habitats to improve their reproductive success (Wootton, 1990).

Reproductive strategies reflect marked differences between species (Wootton, 1984; Murua and Saborido-Rey, 2003), even for billfish species, which present similar processes that govern their reproductive strategies. It is clear, however, that these species have different reproductive strategies due to adaptive mechanisms that allow the fish greater reproductive success. This conclusion is evidenced by our analysis, which identified four groups with distinct reproductive strategies.

CONCLUSION

The major conclusion of our research finding is that billfish present four different reproductive strategies that can be identified based on their growth and how quickly they reach the size or age at first maturity, as well as a differential combination of reproductive characteristics related to fecundity, the frequency and duration of spawning.

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