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## Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantic

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**SUMMARY:** Although information on the spawning seasons of commercially important snappers (Lutjanidae) and groupers (Serranidae, subfamily Epinephelinae) is available for the north and central west Atlantic, there is little information for the tropical western South Atlantic (Brazil). As a consequence, there are few fishery regulations in this entire region that take into consideration such information. In this study, we characterized the reproductive cycles of three Epinephelinae serranids (*Epinephelus morio*, *Mycteroperca bonaci* and *Cephalopholis fulva*) and five lutjanids (*Lutjanus synagris*, *L. jocu*, *L. analis*, *Ocyurus chrysurus* and *Rhomboplites aurorubens*) that occur in the Abrolhos Bank, Brazil, the largest reef complex in the tropical western South Atlantic. A total of 3528 gonads were collected from May 2005 to October 2007. Temporal variability in spawning patterns was evaluated using the Gonadosomatic Index (GSI) and macroscopic analyses. The peak of reproductive activity for the three grouper species occurred between July and August. Snappers exhibited two peaks of reproductive activity, the more intense of which occurred between September and October. The other peak occurred between February and March, with the exception of the deep-dwelling species *R. aurorubens*, which only reproduced between February and March. Seasonal patterns were consistent over the two consecutive years that we studied, and these patterns are equivalent to those observed for the Northern Hemisphere, as are the sizes at maturity and at the time of sexual change (for the three protogynous hermaphrodite groupers). Fisheries management in this region could be significantly improved by a combination of catch and effort limitations being imposed during spawning seasons and by overall size limitations, particularly considering that most of the fish caught are generally below size at maturity. The proposed buffer zones for the marine areas that are presently protected in Abrolhos represent an opportunity for implementing both spatial (e.g. setting no-take zones that cover spawning sites) and temporal (e.g. seasonal closures during spawning peaks) management tools, using a participatory approach at the regional scale.

**Keywords:** small-scale fisheries management, reproduction, reef fisheries, Abrolhos Bank, Brazil.

**RESUMEN:** PATRONES DE DESOVE DE PECES DE ARRECIFE COMERCIALMENTE IMPORTANTES (LUTJANIDAE Y SERRANIDAE) EN EL ATLÁNTICO TROPICAL SUROCCIDENTAL. – A pesar de que se tiene un buen conocimiento sobre la época de freza de los pargos (Lutjanidae) y los meros (Serranidae, subfamilia Epinephelinae) en las zonas norte y central del Atlántico occidental, la información disponible del Atlántico suroccidental es escasa. Como consecuencia, en esta zona aún existen pocas regulaciones pesqueras que tengan en cuenta esta información. En este estudio se caracterizan los ciclos reproductores de tres serránidos Epinephelinae (*Epinephelus morio*, *Mycteroperca bonaci* and *Cephalopholis fulva*) y cinco pargos (*Lutjanus synagris*, *L. jocu*, *L. analis*, *Ocyurus chrysurus* and *Rhomboplites aurorubens*) en el Banco de Abrolhos, el mayor complejo de arrecifes del Atlántico suroccidental. Se examinaron un total de 3528 gónadas entre mayo de 2005 y octubre de 2007. La variabilidad temporal de las pautas de puesta se evaluó mediante el Índice Gonadosomático (GSI) y análisis microscópicos. Para los tres meros el máximo en la actividad reproductora se produce entre julio y agosto. Los lutjánidos presentan dos picos

de actividad bien diferenciados, siendo el más intenso el que tiene lugar entre septiembre y octubre, mientras que el menor se produce entre febrero y marzo, con la excepción de *R. aurorubens*, una especie de profundidad, que sólo se reproduce entre febrero y marzo. Las pautas estacionales en la reproducción son consistentes en los dos años consecutivos y, junto a la edad de primera madurez y la edad de inversión sexual (los tres meros son hermafroditas proterogínicos), son equivalentes a las que se producen en el hemisferio septentrional. La gestión pesquera en esta región podría mejorar significativamente mediante una combinación de limitaciones en las capturas y en el esfuerzo durante las épocas de puesta, así como limitando la talla mínima de captura, considerando que la mayoría de individuos capturados actualmente son inmaduros. Las zonas de amortiguación de las áreas marinas actualmente protegidas en Abrolhos representan una buena oportunidad para implementar herramientas de gestión tanto espaciales (e.g. estableciendo zonas de exclusión pesquera en los lugares de freza) como temporales (e.g. prohibiendo la pesca durante la época de reproducción), utilizando una aproximación participativa a una escala regional.

*Palabras clave:* gestión de pesquerías a pequeña escala, reproducción, pesquerías en los arrecifes, banco de Abrolhos, Brasil.

## INTRODUCTION

Fish from the families Lutjanidae (snappers) and Serranidae, and in particular members of the subfamily Epinephelinae (groupers), comprise some of the most important fishery resources in the tropical west Atlantic and also play a major role as predators in reef ecosystems (Allen, 1985; Polovina and Ralston, 1987; Heemstra and Randall, 1993; Claro *et al.*, 2001). Due to several similarities regarding fishing grounds and gear, as well as their long-lived and large-sized nature, these species are referred to collectively as the “snapper–grouper complex” (e.g. Coleman *et al.*, 1999, 2000; Gobert *et al.*, 2005). Following worldwide trends for marine fisheries (Pauly *et al.*, 2005; Pauly, 2009), most snapper–grouper fisheries are sharply declining, collapsing or already depleted (Morris *et al.*, 2000; Frédoú and Ferreira, 2005). This trend includes fisheries that have been intensively researched and managed (Coleman *et al.*, 2000). Due to the concentrated nature of reproductive events for several species in this group, spawning aggregations of snappers and groupers are currently disappearing even before scientists and managers realize that they exist (e.g. Colin *et al.*, 2003; Sadovy de Mitcheson *et al.*, 2008).

Fifteen species of snappers and 18 species of Epinephelinae groupers occur off the tropical coast of Brazil (Menezes *et al.*, 2003). All but one snapper species is shared with the North and Central Atlantic (Moura and Lindeman, 2007). Though Brazil encompasses a major portion of the distribution ranges of several commercially important West Atlantic reef fish (Moura, 2003), information about their biology, spawning patterns and fisheries in the Southern Hemisphere is still limited, and information about reproductive cycles is restricted to only a few species and localities (Gesteira and Rocha, 1976 and Sousa-Junior *et al.*, 2008 – *Lutjanus synagris*; Teixeira *et al.*, 2004 – *Mycteroperca bonaci*; Costa *et al.*, 2003, 2005 – *Ocyurus chrysurus*; Gerhardinger *et al.*, 2009 – *Epinephelus itajara*). It is of note that there is a bias towards biological studies of the southern red snapper, *Lutjanus purpureus* (e.g. Gesteira and Ivo, 1973; Furtado-Junior and Brito, 2002; Souza *et al.*, 2003), which is a species that sustained important fisheries during the 1960s and 1970s and which is now of minor commercial importance due to overfishing of its main reproductive areas in Brazil (Rezende *et al.*, 2003; Frédoú *et al.*, 2009).

Comparing intraspecific variation in spawning patterns among geographically separated regions provides clues for identifying biological, climatic and oceanographic factors that influence the reproductive patterns of snappers and groupers (e.g. Manickchand-Heileman and Phillip, 1999; Claro *et al.*, 2001). This information can also be used to develop valuable management strategies for multispecific fisheries that encompass different geographical regions. In this study, we present the first multi-species assessment of spawning patterns within the poorly studied Brazilian snapper–grouper complex based on a two-year sampling program in the Abrolhos Bank, the largest and richest coral reef complex in the South Atlantic (Moura and Francini-Filho, 2006). We compared the considerable amount of information regarding reproductive patterns of snappers and groupers in the North and Central Atlantic (e.g. Munro *et al.*, 1973; Coleman *et al.*, 1999, 2000; Claro *et al.*, 2001; Claro and Lindeman, 2003; Colin *et al.*, 2003) with our data and with other data from the western South Atlantic, providing the first multi-species appraisal of whether western South Atlantic spawning patterns are equivalent to those in the northwestern Atlantic. We emphasize the need for regional level management measures, such as size and seasonal restrictions, to complement the fleet regulations recently proposed by Frédoú *et al.* (2009a, b).

## MATERIALS AND METHODS

### Study region

Brazilian reefs are a conservation priority in the Atlantic Ocean due to high endemism levels (about 25% in fish and 50% in corals) that are concentrated in only 5% of West Atlantic reefs (Moura, 2003). Artisanal small-scale fisheries account for an estimated 70% of total fish landings on Brazil’s northeastern coast, and these mainly target demersal reef and shore fish and lobsters (Cordell, 2006; Frédoú *et al.*, 2006). This study was carried out in the Abrolhos Bank, Bahia State, which covers a wide part (46000 km<sup>2</sup>) of the continental shelf. The shelf rarely exceeds 30 m, and the shelf edge is at approximately 70 m depth (16°40’–19°40’S, 39°10’–37°20’W; Fig. 1). The study region comprises the largest and richest coral reefs in the South Atlantic, with nearly 300 species of fish and 20 species of reef-building corals, as well as an extensive mosaic of algal

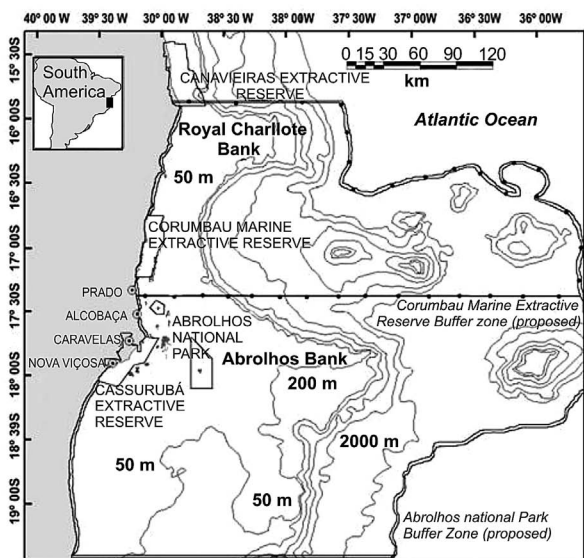


FIG. 1. – Map of the study region showing the Royal Charlotte Bank and the Arolhos Bank, as well as the marine protected areas and shallow (<30 m) coral reefs.

bottoms, mangrove forests, beaches and vegetated sandbanks (Moura and Francini-Filho, 2006). Nearly 20000 artisanal fishermen operate in the Arolhos Bank, but little is known about the region's fisheries and these were not included in recent revisions of data on reef fisheries in northeastern Brazil (Frédou *et al.*, 2006, 2009a, b).

### Sampling and analytical methods

Monthly surveys focusing on hand line, longline and spearfishing landings were carried out at the four main coastal municipalities within the study region (Prado, Alcobaca, Caravelas and Nova Viçosa; Fig. 1) between May 2005 and July 2007. Specimens were measured to the nearest millimetre (total and standard length, TL and SL respectively), sexed, and weighed to the nearest 0.1 g, including total and gutted weight (TW and GW respectively) and gonad weight (GNW). Comparisons with data from the literature were based on fork lengths (FL). Maturity was detected macroscopically based on gonad size, consistency, colour, vascularization, presence of lateral sperm sinuses, ovarian cavity, ovarian lamellae and identifiable oocytes (Munro, 1983; Colin *et al.*, 2003). Sex ratio was estimated using the operational criterion (i.e. only adults included) (Polovina and Ralston, 1987).

The seasonality of gonad development was analyzed with the Gonadosomatic Index (GSI). Analysis of Covariance (ANCOVA) was used to evaluate the monthly variation in the GSI, with log-transformed values of GW for females as covariates, the month as the main effect, and log-transformed values of GNW as the dependent variable. Since body size was positively correlated with GW values for all species studied, the covariance model was used to estimate GSI for each month.

The smallest size class at which 50% of fish were sexually mature ( $L_{50}$ ) was estimated separately for males and females by fitting the logistic function with a maximum likelihood estimation (Roa, 1993), using the following binomial likelihood function:

$$L(\hat{p} | x) = \sum_{i=1}^M x_i \ln(\hat{p}_i) + (n_i - x_i) \ln(1 - \hat{p}_i)$$

where  $\hat{p}$  is the predicted maturity at length class  $i$  given by the logistic function,  $x_i$  is the number of mature fish,  $n_i$  is the total number of fish in length class  $i$ , and  $M$  is the total number of size classes. Calculations were performed using the ADFM software (Otter-Research, 2000). For species with a limited sample size, the maximum size of immature specimens and the minimum size of mature specimens were assessed. Size at sexual transformation for the three protogynous hermaphrodite serranids was first estimated by examining sex-related length frequency distributions.

Semi-structured interviews were carried out with fishermen who had more than ten years of fishing experience in the region, including representatives from Prado, Alcobaca and Caravelas. The interviews were designed to assess local knowledge on temporal and spatial reproductive patterns of snappers and groupers. We asked whether and when each of the studied species spawns and/or forms aggregations. Simple maps of the region were presented during interviews to help fishermen recognize the different fishing grounds. After the results were consolidated, follow-up meetings were convened in the main fishing localities to discuss possible management interventions.

### RESULTS

A total of 3528 specimens were obtained from the four most common snappers (*Lutjanus synagris*, *Lutjanus joco*, *Ocyurus chrysurus*, *Rhomboplites aurorubens*) and the three most common groupers (*Cephalopholis fulva*, *Epinephelus morio*, *Mycteroperca bonaci*) (Table 1). Two other snapper species (*Lutjanus analis*, *Lutjanus vivanus*) and three groupers (*Mycteroperca venenosa*, *Cephalopholis furcifer*, *Alphestes afer*) were only occasionally landed and sampled (169 specimens; Table 1); therefore, the covariance model could not be used for these species.

Gutted weight (GW) covaried significantly with GSI for all species in both families (Table 2), with the exception of *Mycteroperca bonaci*. Temporal variability in GSI values was highly significant for all species, also with the exception of *M. bonaci* (Fig. 2). The weak covariations observed for *M. bonaci* may be related to the low sample size (22 females). Length-weight (LW) and length-length (LL) equations are provided in Table 3.

All lutjanids are gonochoristic (i.e. have separate sexes), and the four species that we studied had a sex ratio approaching 1:1 (Table 1). Spawning of *Lutjanus synagris* spanned from the Southern Hemisphere

TABLE 1. – Total sample size, number of non-immature individuals in the sample, and sex ratio for the most frequent species of snapper (Lutjanidae) and groupers (Serranidae) in the Abrolhos Bank reef fisheries. The \* indicates species included in the GSI analyses.  $p_{\text{♀}}$  refers to the proportion of females, se is the standard error of  $p_{\text{♀}}$ .

	N	n (non-immature)		sex ratio	$P_{\text{♀}}$	se
		♀	♂			
<b>Lutjanidae</b>						
<i>Lutjanus synagris</i> *	770	354	259	1.4	0.46	0.02
<i>Ocyurus chrysurus</i> *	619	272	177	1.5	0.44	0.02
<i>Rhomboplites aurorubens</i> *	487	254	228	1.1	0.52	0.02
<i>Lutjanus jocu</i> *	315	60	109	0.6	0.19	0.02
<i>Lutjanus analis</i>	102	5	16	0.3	0.05	0.02
<i>Lutjanus vivanus</i>	38	19	16	1.2	0.49	0.08
<b>Serranidae</b>						
<i>Cephalopholis fulva</i> *	750	623	107	5.8	0.83	0.01
<i>Epinephelus morio</i> *	302	131	33	4.0	0.43	0.03
<i>Mycteroperca bonaci</i> *	116	22	12	1.8	0.19	0.04
<i>Cephalopholis furcifer</i>	15	9	6	1.5	0.60	0.13
<i>Mycteroperca venenosa</i>	8	2	2	1.0	0.25	0.15
<i>Alphestes afer</i>	6	5	0		0.83	0.15

TABLE 2. – Summary of the ANCOVA results with female log-transformed gutted weight (GW) as covariate, month as the main effect, and log-transformed gonad weight as dependent variable (ns non-significant  $p > 0.10$ , \*  $p \leq 0.10$ , \*\*  $p \leq 0.5$ ).

Species	Log (gutted weight)		Month		df	Residuals		$R^2$
	MS	F	MS	F		MS	df	
<b>Lutjanidae</b>								
<i>Lutjanus synagris</i>	130.65	280.02 **	7.68	16.46 **	25	0.47	337	0.67
<i>Ocyurus chrysurus</i>	437.74	649.25 **	23.71	35.17 **	12	0.67	315	0.77
<i>Rhomboplites aurorubens</i>	29.65	153.31 **	6.25	32.32 **	17	0.19	234	0.75
<i>Lutjanus jocu</i>	27.50	34.90 **	27.50	9.12 **	13	0.79	45	0.70
<b>Serranidae</b>								
<i>Cephalopholis fulva</i>	34.84	73.85 **	32.15	68.15 **	15	0.47	566	0.73
<i>Epinephelus morio</i>	38.39	33.82 **	7.77	6.84 **	19	1.14	110	0.60
<i>Mycteroperca bonaci</i>	0.826	0.60 ns	3.06	2.23 *	9	1.37	11	0.65

spring to summer, with maximum GSI values recorded from September to March (Fig. 2). Spawning of *Lutjanus jocu* and *Ocyurus chrysurus* spanned from the Southern Hemisphere winter to spring, with maximum GSI values observed from June to October and from August to October respectively. A smaller GSI peak was also detected between February and March for both *L. jocu* and *O. chrysurus*. In contrast with the three aforementioned lutjanids that occur in shallow coastal areas, spawning of the deep-reef dweller *Rhomboplites aurorubens* occurred between the Southern Hemisphere summer and early autumn, with maximum GSI values from February to April (Fig. 2). Maturity data for the two rarer lutjanids are summarized in Table 1. Five mature females of *Lutjanus analis* were collected, three in June 2006, one in November 2006 and one in March 2007. No mature *Lutjanus vivanus* individuals were collected.

The three serranids for which a sufficient sample size was obtained are protogynous hermaphrodites, with gonads functioning first as ovaries and then transforming into testes (e.g. Brulé *et al.*, 2003; Giménez-Hurtado *et al.*, 2003), resulting in sex ratios that are biased towards smaller females (Table 1). Spawning in these species extended from the Southern Hemisphere winter to spring, with GSI values peaking from June to September for *Cephalopholis fulva* and *Epinephelus morio*, and from August to September for *Mycteroperca*

*bonaci* (Fig. 2). For these three species, the inclusion of non-immature males in the analyses did not affect the results. The maturity data for the rarest serranids are summarized in Table 1. Seven mature *Cephalopholis furcifer* females were collected in August and October 2005. Two mature *Mycteroperca venenosa* females were collected in September 2006. Two mature *Alphestes afer* females were collected in June and another one (spent) in November 2005.

Size at maturity ( $L_{50}$ ) was estimated separately for each sex and is summarized in Table 4 for the six most common species. Maturity ogives are presented in detail in Figure 4. The small sample sizes of the remaining rarer species made it impossible to estimate  $L_{50}$ , but there are relevant clues from the material examined. For *Rhomboplites aurorubens*, the smallest non-immature specimens were 14.7 (female) and 16.5 cm SL (male), while the largest immature specimens were 17.5 (female) and 15.3 cm SL (male), which suggests that  $L_{50}$  would be close to these values (Table 4). Similarly,  $L_{50}$  for *Lutjanus analis* may range from 31.2 to 40 (females) and from 28.9 to 29.5 cm SL (males); for *Lutjanus vivanus*,  $L_{50}$  may range from 23.7 to 26 (females) and from 22.7 to 24 cm SL (males); for *Mycteroperca venenosa*,  $L_{50}$  for females is likely to be between 49.5 and 63 cm SL. For *Cephalopholis furcifer*, the smallest non-immature female was 18.5 cm SL, but no immature individuals were found. Only females

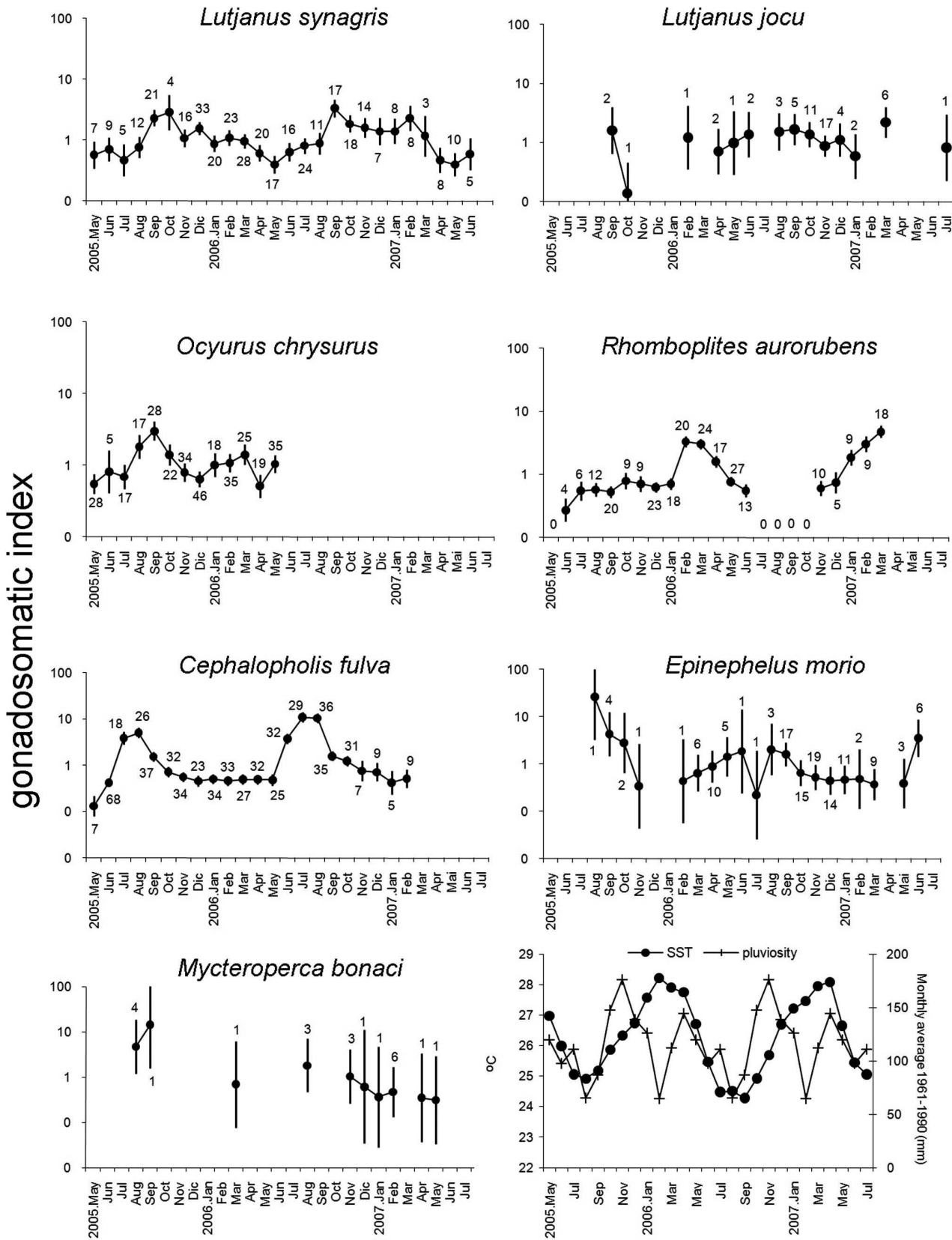


FIG. 2. – Temporal variation in the Gonadosomatic Index (GSI) for seven commercially important reef fish species, as well as for air temperature and rainfall. Estimates of the expected GSI values (dots) and their 95% confidence limits (bars).

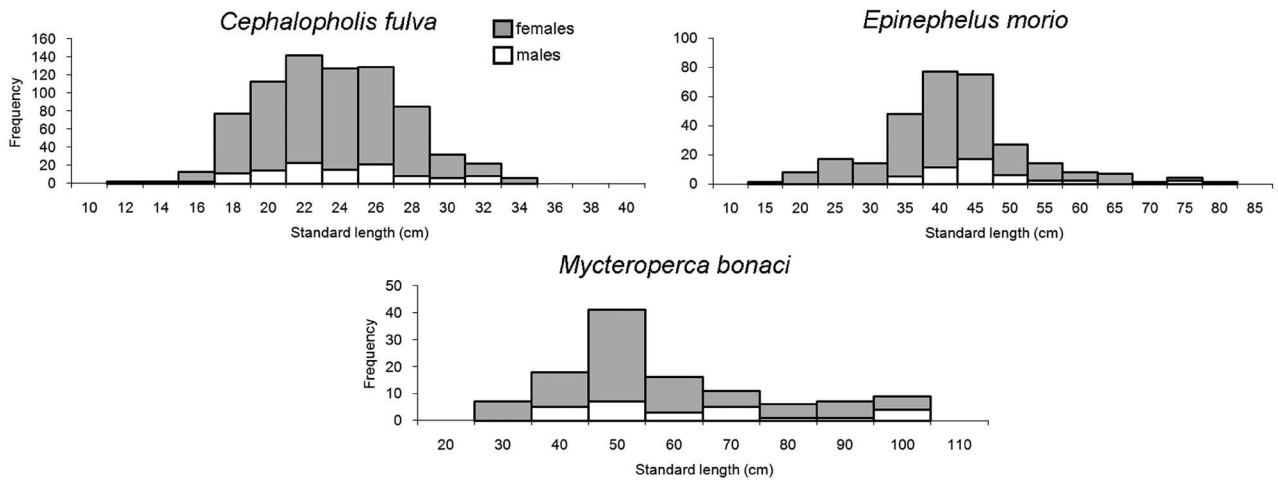


FIG. 3. – Proportion of males and females in different size categories for three commercially important reef fish species.

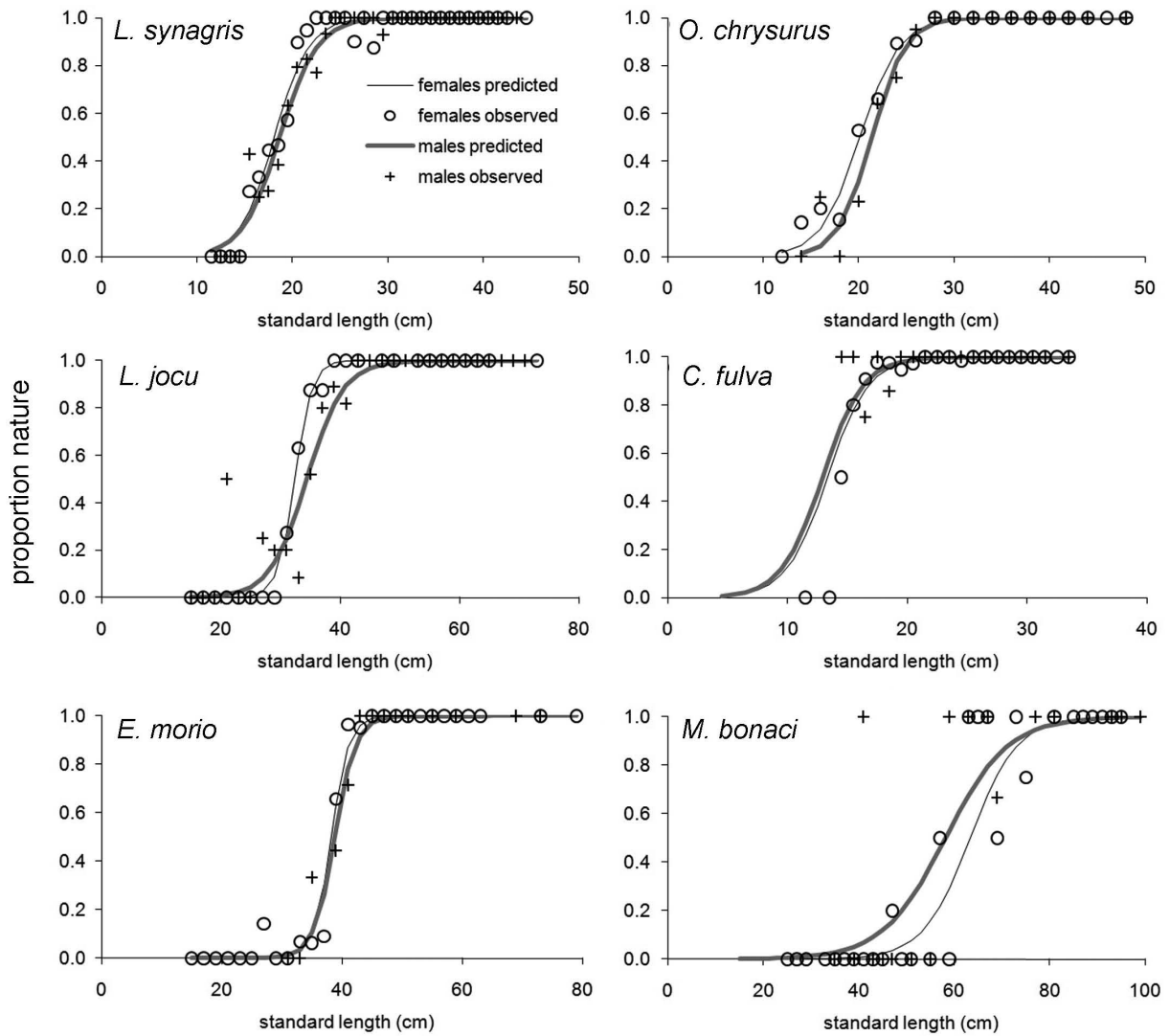


FIG. 4. – Observed and predicted values of size at maturity (L<sub>50</sub>) for the six most common commercially important reef fish species in the study region.

TABLE 3. – Size range, Standard Length-Weight (SL-W) and Total Length - Standard Length (TL-SL) relationships for the eleven most common lutjanids and serranids studied in the Abrolhos Bank, Brazil.

Species	Standard length (mm) range	log(W) ~ log (SL)		TL ~ SL		SL ~ TL	
		intercept	slope	intercept	slope	intercept	slope
<b>Lutjanidae</b>							
<i>Lutjanus synagris</i>	11.4 – 45.3	-2.93256	2.79322	1.33393	1.21109	-0.87414	0.81880
<i>Ocyurus chrysurus</i>	12.1 – 50.3	-3.20386	2.85286	0.75278	1.36745	0	0.71749
<i>Rhomboplites aurorubens</i>	13.7 – 37.0	-3.01855	2.80358	0.49616	1.27843	0	0.76828
<i>Lutjanus jocu</i>	11.1 – 69.5	-3.00117	2.85376	1.80074	1.20823	-1.22331	0.82149
<i>Lutjanus analis</i>	13.7 – 70.0						
<i>Lutjanus vivanus</i>	19.7 – 47.0						
<b>Serranidae</b>							
<i>Cephalopholis fulva</i>	11.9 – 33.6	-3.29401	2.95492	0.99399	1.16289	-0.72689	0.85524
<i>Epinephelus morio</i>	12.0 – 78.5	-3.51953	2.97117	2.20823	1.17718	-1.23918	0.83637
<i>Mycteroperca bonaci</i>	24.2 – 99.0	-3.54946	2.98008	2.20823	1.17718	-1.23918	0.83637
<i>Cephalopholis furcifer</i>	18.5 – 27.4						
<i>Mycteroperca venenosa</i>	30.1 – 65.0						

TABLE 4. – Summary data for the most frequent species of snapper (Lutjanidae) and groupers (Serranidae) in the Abrolhos Bank reef fisheries.

Species	Smallest non-immature specimen (mm)		Largest immature specimen (mm)		L <sub>50</sub> (mm) (± SE)		Sampling period	Depth (m)	
	♀	♂	♀	♂	♀	♂		Observed	Literature range (maximum)
<b>Lutjanidae</b>									
<i>Lutjanus synagris</i> *	15.7	15.5	21.5	23.3	18.11 (±0.36)	18.67 (±0.39)	May 2005-Jun 2007	5-40	400 <sup>1</sup>
<i>Ocyurus chrysurus</i> *	14.7	16	25.3	25.4	20.15 (±0.44)	21.39 (0.51)	May 2005-Jun 2006	5-150	180 <sup>1</sup>
<i>Rhomboplites aurorubens</i> *	14.7	16.5	17.5	15.3	<sup>3</sup>	<sup>3</sup>	May 2005-Mar 2007	15-150	300 <sup>1</sup>
<i>Lutjanus jocu</i> *	30.5	26.6	36	40	32.42 (±0.49)	34.42 (0.74)	May 2005-Jul 2007	5-150	40 <sup>1</sup>
<i>Lutjanus analis</i>	40	28.9	31.2	29.5	<sup>3</sup>	<sup>3</sup>	May 2005-Mar 2007	5-200	100 <sup>1</sup>
<i>Lutjanus vivanus</i>	23.7	24	26	22.7	<sup>3</sup>	<sup>3</sup>	Set 2005-Dec 2006	40-300	242 <sup>1</sup>
<b>Serranidae</b>									
<i>Cephalopholis fulva</i> *	14.3	14.2	24.5	18.3	13.33 (±0.93)	12.91 (±3.07)	May 2005-Feb 2007	40-150	150 <sup>2</sup>
<i>Epinephelus morio</i> *	28	38.5	42.2	42	38.19 (±0.35)	38.77 (±0.91)	May 2005-Jul 2007	5-200	330 <sup>2</sup>
<i>Mycteroperca bonaci</i> *	46.5	41.4	70	70	63.33 (±2.57)	58.14 (±4.32)	May 2005-Jul 2007	5-300	33 <sup>2</sup>
<i>Cephalopholis furcifer</i>	18.5	19			<sup>3</sup>	<sup>3</sup>	Jun 2005-Feb 2006	50-300	100 <sup>2</sup>
<i>Mycteroperca venenosa</i>	63	46	49.5	-	<sup>3</sup>	<sup>3</sup>	Jun 2005-Mar 2007	20-200	137 <sup>2</sup>
<i>Alphestes afer</i>	18.4		17.5	-	<sup>3</sup>	<sup>3</sup>	Jun 2005-Abr 2006	40-150	30 <sup>2</sup>

<sup>1</sup> Allen, 1985; <sup>2</sup> Heemstra and Randall, 1993; <sup>3</sup> small sample size precluded L<sub>50</sub> estimation.

of *Alphestes afer* were collected, and the smallest non-immature individual was 18.4 cm SL and the largest immature individual was 17.5 cm SL.

Size at sexual transformation for the three most common groupers is summarized in Figure 3, showing that *Cephalopholis fulva* begins to change sex before it reaches a size of 18 cm SL, *Epinephelus morio* before it reaches 35 cm SL and *Mycteroperca bonaci* after it reaches 40 cm SL. As expected for protogynous fish, the size distribution of males did not overlap with that of females in the smaller size classes.

## DISCUSSION

### Spawning season

Although spawning individuals of most tropical coastal fish species may be found year-round, there may be discernible regional patterns of reproductive timing in snappers and groupers (Munro, 1983; García-Cagide *et al.*, 2001; Claro *et al.*, 2009). The seasonal spawning patterns that we report here for the Abrolhos Bank are highly equivalent to those known for the western North Atlantic and are compatible with the results of other studies from Brazil. Potential biases due to the lack of

histological analyses for confirming the macroscopically assessed maturity stages were minimized by our two-year sampling period, as the second year corroborated the results from the previous year in all cases.

In Abrolhos, the maximum GSI values for *Lutjanus synagris* ranged from late winter (September) to late summer (March). This result is fully compatible with the results from Gesteira and Rocha (1976) and partially matches the findings of Sousa-Junior. *et al.* (2008), who found a secondary peak in spring (August-November) and a more pronounced peak during the summer (January-March), when we detected only a secondary GSI peak in Abrolhos (17°S) (Fig. 2). Both Gesteira and Rocha (1976) and Sousa-Junior. *et al.* (2008) studied populations from Ceará State (3-5°S), Brazil, and it is expected that some latitudinal variation occurs within regions/hemispheres (see *Lutjanus jocu* and *Rhomboplites aurorubens* below). In Cuba and Mexico, *L. synagris* is reported to spawn from late winter to early autumn (García-Cagide *et al.*, 2001), in May in the Gulf of Batabano and the northwest shelf, and in June in the south and northeast zones of the Cuban platform (Claro and Lindeman, 2003; Claro *et al.*, 2009); while, in Venezuela, most reproductive activity for this species is reported from the early sum-

mer (July) to mid-autumn (November) (Gómez *et al.*, 2001), in agreement with the idea that spawning peaks can vary within regions. For *Lutjanus jocu* and *Ocyurus chrysurus*, the GSI peaks in Abrolhos ranged from late autumn to early spring (June to October). While there are no data for other Brazilian populations of *L. jocu*, the spring reproductive peak that was reported for *O. chrysurus* by Costa *et al.* (2005) in Porto Seguro (the northern part of the Abrolhos Bank) was in full agreement with our data. Compared with Caribbean seasonal spawning patterns (Claro, 1983; Munro, 1983; Polovina and Ralston, 1987; García-Cagide *et al.*, 2001; Claro *et al.*, 2009), the spawning seasons that we observed only partially overlap, as both *L. jocu* and *O. chrysurus* tend to spawn in the Northern Hemisphere between late winter and early autumn (i.e. February to October). For *O. chrysurus*, the spawning peak in the Gulf of Batabano was observed during May and June, while in the northwest region of Cuba, it occurs in April and May (Claro, 1983).

In contrast with the more coastal lutjanids, the GSI values for the deeper-dwelling species *Rhomboplites aurorubens* peaked in Abrolhos between the Southern Hemisphere summer and autumn (February to May). While there have not been any reproductive studies on *R. aurorubens* in Brazil, in the Southern United States and eastern Gulf of Mexico this species is known to spawn between spring and late summer (May to September) (Cuellar *et al.*, 1996; Hood and Jonshon, 1998), and *R. aurorubens* spawns throughout the year in Trinidad and Tobago (Manickchand-Heileman and Phillip, 1999). Higher reproductive activity was found to be associated with the wet season in Trinidad and Tobago, from June to November (Manickchand-Heileman and Phillip, 1999). While seasonal variation in water temperature may be the predominant spawning trigger at higher latitudes, factors such as rainfall may explain some of the latitudinal or regional incongruence in spawning patterns in tropical regions. In Abrolhos, there is a strong correspondence between spawning and rain/temperature peaks for *R. aurorubens* (Fig. 2). However, it is currently impossible to discriminate between the many potentially interacting environmental factors that influence intra- and inter-regional seasonal reproductive patterns of *R. aurorubens* and of the other species in this study. The factors involved may include water temperature, photoperiod, food abundance, temperature, rainfall (which affects the salinity in coastal areas) and the strength of prevailing currents (Wootton, 1998).

In Abrolhos, the reproductive peaks of serranids were much more homogeneous than those found for lutjanids, which had maximum GSI values recorded between the Southern Hemisphere winter and spring (June to September) for *Cephalopholis fulva*, *Epinephelus morio* and *Mycteroperca bonaci*. For *M. bonaci*, which is the only tropical grouper species for which there are spawning data from Brazil, Teixeira *et al.* (2004) recorded coincident spawning peaks between 2 and 10°S, with females being fertile between

August and September. The breeding seasons of these three serranids in Brazil largely correspond to those that have been recorded in the Northern Hemisphere (Smith, 1961; Moe, 1969; Munro, 1983; García-Cagide and García, 1996; Brulé *et al.*, 1999; Giménez-Hurtado *et al.*, 2003; Burgos *et al.*, 2007), where they also tend to spawn from late autumn to early spring (December to April). Information from larval assemblages that have been studied on the Abrolhos Bank (Nonaka *et al.*, 2000) shows the increased abundance of larval groupers during the winter, when they are among the five most abundant larval fish families. Larval snappers are rare throughout the year (Nonaka *et al.*, 2000), which could reflect their larval behavioural characteristics and cross-shelf distribution.

Although the spawning periods of the rarer species could not be estimated precisely based on our data, there is some agreement between the data that have been reported in the literature from the Northern Hemisphere and the few mature specimens of *Lutjanus analis*, *Alphestes afer*, *Mycteroperca venenosa* and *Cephalopholis furcifer* that we collected in Abrolhos. As there are no other data from Brazil, the fragmentary information presented herein is useful as a base for preliminary comparison. Additional studies may confirm that *L. analis* spawns between spring and autumn in the Southern Hemisphere (reported to spawn from April to August in Cuba; Claro *et al.*, 2001; Claro *et al.*, 2009), while the grouper species *A. afer*, *M. venenosa* and *C. furcifer* spawn during the Southern Hemisphere winter (reported to spawn between December and May in the Caribbean; Thompson and Munro, 1974).

### Size at maturity

The smallest size class at which 50% of fish were sexually mature ( $L_{50}$ ) for *Lutjanus synagris* (18.1-18.7 cm SL for females and males respectively) is similar to records from the central Caribbean (Thompson and Munro, 1974; Claro *et al.*, 2001) and is slightly smaller than the size reported in Venezuela (Gómez *et al.*, 2001) and Bermuda (Luckhurst *et al.*, 2000). The values reported by Sousa-Junior *et al.* (2008) from Ceará State (3-5°S), Brazil, completely agree with our estimates. For *Ocyurus chrysurus*, our  $L_{50}$  estimates ranged between 20.2 and 21.4 cm SL (females and males), but it is difficult to compare our results with those from previous studies as published records vary greatly, and range from 13-17 cm FL (Piedra-Catañeda, 1965; Claro *et al.*, 2001) to 26 cm FL (Thompson and Munro, 1974). In the northern part of the Abrolhos Bank, Costa *et al.* (2005) reported an  $L_{50}$  ranging from 18.6 to 22.4 cm FL, which is very close to our estimates. For *Lutjanus jocu*, our  $L_{50}$  estimates (32.4-34.4 cm SL for females and males) are similar to those from the Central Caribbean (Thompson and Munro, 1974) and slightly lower than those from Cuba (García-Cagide *et al.*, 2001: 43-48 cm FL). Thompson and Munro (1974) suggested that *Cephalopholis fulva* at-



tains maturity before reaching 16 cm TL, which is very similar to our estimates for Abrolhos (13.33-12.91 cm SL, females and males). For *Epinephelus morio*, our  $L_{50}$  estimates (38.2-38.8 cm SL, females and males) are comparable to data from the Caribbean (Burgos *et al.*, 2007: 48.7 cm TL), and for *Mycteroperca bonaci*, our  $L_{50}$  estimates (58.1-63.3 cm SL, females and males) are comparable to data from Florida (Crabtree and Bullock, 1998: 50.8 cm TL), Cuba (García-Cagide and García, 1996: 57 cm TL) and Mexico (Brulé *et al.*, 2003: 72.1 cm TL) (females only). In addition to being influenced by intrinsic regional variation, the  $L_{50}$  may also be affected by external factors such as exploitation level, as has been reported for *L. synagris* in Cuba by Claro *et al.* (2001), who compared shifts in the timing of sexual maturity that occurred in Cuba between 1960 and 1972 due to overfishing ( $L_{50}$  shifted from 13-16 to 18-20 cm FL). The estimates that we present here provide a broad comparative baseline for Brazil and for future assessments in the Abrolhos Bank.

Although the length at the time of sexual transition for 50% of the population was not estimated in the present study (e.g. Crabtree and Bullock, 1998; Brulé *et al.*, 2003), the minimum sizes of *Cephalopholis fulva* and *Epinephelus morio* in Abrolhos that we measured for them to have undergone sexual transition were very similar to values from the Caribbean. *C. fulva* and *E. morio* begin sexual transition at approximately 18 and 35 cm SL in Abrolhos (22 and 45 cm TL in the Caribbean and the southern United States) (Thompson and Munro, 1974; Burgos *et al.*, 2007). However, *Mycteroperca bonaci* begins changing sex in Abrolhos only after reaching 40 cm SL, which differs from observations from the southern Gulf of Mexico (Brulé *et al.*, 2003: 85 cm FL) but is closer to the smallest size for transitional *M. bonaci* from northeastern Brazil (64 cm FL) that was reported by Teixeira *et al.* (2004). In this case, histological corroboration of our results will be necessary before this geographical variation in size at the time of sexual transition can be confirmed. It is worth noting that fishing of these species is concentrated on immature or only recently matured individuals (see Figs. 3 and 4), which may compromise the long-term sustainability of these fisheries (Myers and Mertz 1998; Claro *et al.*, 2001, 2009; Claro and Lindeman, 2004).

Similarly to what was observed by Crabtree and Bullock (1998) and Brulé *et al.* (2003), we also observed sexual dimorphism in *Mycteroperca bonaci* in Abrolhos. Fin pigmentation was not recorded in all specimens, but jet black pigmentation on the fin was confirmed in at least some of the large males from Brazil.

### Conservation and fishery implications

The most abundant snapper-grouper species that we assessed, including *Lutjanus synagris*, *Lutjanus jocu*, *Ocyurus chrysurus*, *Epinephelus morio* and *Mycteroperca bonaci*, are well known to form spawning aggre-

gations in the Caribbean (Claro and Lindeman, 2003; Claro *et al.*, 2009; Sadovy de Mitcheson *et al.*, 2008). The location and protection of the sites where most spawning occurs over a few months each year would be one of the most significant conservation measures that can be undertaken for these species (Sadovy de Mitcheson *et al.*, 2008). The problem behind implementing these policies lies in the fact that there is no information on the location of the spawning sites of most snappers and groupers, particularly in the regions of large, complex continental shelf environments, such as the Royal Charlotte and Abrolhos Banks in Brazil. Under these circumstances, precautionary management measures need to be implemented even before spawning sites are located and protected. Spawning aggregations, as defined by Colin *et al.* (2003), have not been recorded in Abrolhos until now. However, before we began biological sampling for this study, 30 experienced fishermen were interviewed and were asked specifically whether and when each of the studied species spawns and/or forms aggregations. Responses varied, with less than 50% correspondence between the observed GSI peaks and the responses from fishermen with respect to breeding seasons, with the exception of *L. synagris* and *O. chrysurus*, for which there was more than 90% correspondence. Information about spawning aggregations was even more ambiguous, with the exception of *O. chrysurus*, for which there is well-established knowledge among local fishermen of a spawning ground in the southern part of the Abrolhos Bank. Further assessments in this area are underway to confirm the existence and the characteristics of this potential spawning aggregation site. With the exception of jewfish spawning aggregations in Santa Catarina State (Gerhardinger *et al.*, 2009), there is only speculation on the timing and location of snapper-grouper spawning aggregations in Brazil (Teixeira *et al.*, 2004; Costa *et al.*, 2003, 2005).

All of the species within the snapper-grouper complex were reported by nearly all the interviewed fishermen to have been previously more abundant in the Abrolhos Bank, including *Lutjanus cyanopterus*, *Mycteroperca venenosa* and *Epinephelus itajara*, which were nearly absent from our samples. Previous stock assessments in the study region (Klippel *et al.*, 2005) indicate that *Ocyurus chrysurus* and *Rhomboplites aurorubens* have been severely overfished, and *Lutjanus jocu* and *Lutjanus vivanus* are currently subjected to maximum levels of fishing mortality, while only *Lutjanus synagris* and *Lutjanus analis* are only moderately over-exploited. A similar exploitation situation has been reported for northeastern Brazil between 4 and 13°S (Frédou *et al.*, 2009a, b). Grouper stocks have never been assessed in Brazil, but their state may be even worse than that of snappers (Teixeira *et al.*, 2004).

Besides the implementation of subsidies (Abdallaha and Sumaila, 2007), there has never been a significant public policy for managing reef fisheries in Brazil (e.g.

catch or effort limitations), with the following exceptions: a country-wide ban on catching *Epinephelus itajara* since 2002, size limits for *Lutjanus purpureus* in northern and northeastern Brazil, and size limits for *Epinephelus niveatus*, *Mycteroperca marginata* and *Mycteroperca acutirostris* in southern and southeastern Brazil. Coastal environmental and fishery management in the Abrolhos region, which contains the largest and richest South Atlantic reef system, is centred on Marine Protected Areas (MPAs) under no-take (~890 km<sup>2</sup>) and multiple-use regimes (~2908 km<sup>2</sup>) (Fig. 1). There is growing evidence of the positive effects for Abrolhos of zoning and management within MPAs (Moura *et al.*, 2007; Francini-Filho and Moura, 2008a), and spillover of snappers and groupers from no-take zones has been demonstrated on a local scale (hundreds of meters) (Francini-Filho and Moura, 2008b). However, the present as well as other studies suggest that managing reef fisheries only within the existing MPAs will not reverse the current declining trend.

Though the MPA networks do not encompass all if any of the spawning aggregation sites (generally deep reefs near the shelf break; Sadovy de Mitcheson *et al.*, 2008), and larger snapper-groupers are caught far outside the MPA limits (see Table 4; note that no MPA reaches depths >20 m) and in areas that benefit from spillover from no-take zones (Francini-Filho and Moura, 2008b), the buffer zones that have been proposed around MPAs should provide an adequate framework for managing reef fisheries. Within Brazilian legislation consultative and deliberative councils must be set up for MPAs, with their jurisdiction extending over the buffer zones. Councils are one of the few instances in which the people managing fisheries receive direct and continuous input from fishermen, and this is especially true in Extractive Reserves, where the councils are deliberative (e.g. Corumbau, Cassurubá, and Canavieiras in the Abrolhos Region). These co-management arrangements are some of the few success stories of small-scale fisheries management in Brazil (Seixas *et al.*, 2009). It is important to highlight that the implementation of buffer zones would facilitate establishing both spatial (e.g. new no-take areas covering spawning sites) and temporal (e.g. seasonal closures) management tools. In fact, because no spawning aggregation sites are currently known, seasonal closures during spawning peaks may be a more effective alternative. The information provided herein regarding lengths at first sexual maturity and spawning periods can therefore be readily incorporated into management plans for MPAs (see Moura *et al.*, 2007; Francini-Filho *et al.*, 2008a, b).

The L<sub>50</sub> estimates we calculated based on our observations were shown to more than 300 fishermen from six communities in 2007 (public meetings with 20 to 60 attendees), and there was a general consensus on the declining status of the snapper-grouper fisheries and on the need for setting minimum size limits for catches (maximum size limits were considered an unreach-

able target). Restrictions on fishing during spawning peaks may be more complex to implement due to the non-selective nature of the snapper-grouper fisheries combined with their relatively long spawning seasons. Nonetheless, the species that we observed do exhibit discernible spawning peaks, and seasonal restrictions must at least be considered and further discussed among the stakeholders (September to October for lutjanids, except for *Rhomboplites aurorubens*, and July to August for serranids).

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