



Abstract—The hooded slipper lobster (*Scyllarides deceptor*) and Brazilian slipper lobster (*S. brasiliensis*) are commonly caught by fishing fleets (with double-trawling and longline pots and traps) off the southeastern coast of Brazil. Their reproductive biology is poorly known and research on these 2 species would benefit efforts in resource management. This study characterized the population structure of these exploited species on the basis of sampling from May 2006 to April 2007 off the coast of Santos, Brazil. Data for the absolute fecundity, size at maturity in females, reproductive period, and morphometric relationships of the dominant species, the hooded slipper lobster, are presented. Significant differential growth was not observed between juveniles and adults of each sex, although there was a small investment of energy in the width and length of the abdomen in females and in the carapace length for males in larger animals (>25 cm in total length [TL]). Ovigerous females were caught more frequently in shallow waters in August–September than in January–February, indicating a possible migration to spawn. Fecundity ranged from 55,800 to 184,200 eggs (mean fecundity: 115,000 [standard deviation 43,938] eggs). The spawning period occurred twice a year, with a higher relative frequency between July and October, and the length at 50% maturity for females was ~25 cm TL; both these findings should be considered by resource managers. Proper management of catches of slipper lobsters is important because of the high economic value of this fishery.

Manuscript submitted 18 June 2013.
Manuscript accepted 2 December 2014.
Fish. Bull. 113:55–68 (2015).
doi: 10.7755/FB.113.1.6

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Slipper lobsters (Scyllaridae) off the southeastern coast of Brazil: relative growth, population structure, and reproductive biology

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Few species-specific fisheries worldwide exist for the slipper lobsters (Scyllaridae), in contrast to those for the spiny lobsters (Palinuridae) and clawed lobsters (Nephropidae), although some slipper lobsters have significant commercial value (Spanier and Lavalli, 2007; Duarte et al., 2010). According to Holthuis (1991), of the 85 species of lobsters recorded (see Lavalli and Spanier, 2007), 35.3% are of commercial interest, and of these interest has increased in species of the genus *Scyllarides*, such as the Brazilian slipper lobster (*S. brasiliensis*), Mediterranean slipper lobster (*S. latus*), and blunt slipper lobster (*S. squamosus*). In addition, other species of Scyllaridae have commercial value, including 4 species of the genus *Ibacus*, the velvet fan lobster (*I. altricrenatus*), Japanese fan lobster (*I. ciliatus*), smooth fan lobster, (*I. novemdentatus*), and butterfly fan lobster (*I. peronii*), as

well as the sculptured mitten lobster (*Parribacac antarcticus*) and flathead lobster (*Thenus orientalis*).

The reproductive biology of members of the Scyllaridae (Lavalli and Spanier, 2007) has been studied for the genera *Thenus* (Kagwade and Kabli, 1996; Courtney et al., 2001) and *Ibacus* (Stewart et al., 1997; Haddy et al., 2005) with emphasis on the genus *Scyllarides* (Hardwick and Cline, 1990; Spanier and Lavalli, 1998; DeMartini and Williams, 2001; DeMartini et al., 2005; Hearn and Toral-Granda, 2007; Oliveira et al., 2008). According to the above mentioned authors, the sizes of females at maturity are smaller in species of the genera *Ibacus* (butterfly fan lobster) and *Thenus* (flathead lobster and *T. indicus*) than in species of the genus *Scyllarides* (blunt slipper lobster, Galapagos slipper lobster [*S. astori*], and hooded slipper lobster [*S. deceptor*]). Moreover, species of *Iba-*

cus and *Thenus* show lower fecundity than species of *Scyllarides*.

A new, species-specific study for the hooded slipper lobster is needed to gain a better understanding of biological patterns in this species. The variability in the reproductive biology of species of *Scyllarides* has been shown to be relatively high. For example, the hooded slipper lobster has 2 spawning seasons per year (Oliveira et al., 2008)—a difference from the Galapagos slipper lobster (Hearn and Toral-Granda, 2007)—and a mean tail width at maturity of 62.6 mm (Oliveira et al., 2008), compared with a mean tail width of 47.6 mm for the blunt slipper lobster (DeMartini et al., 2005). Studies of *Scyllarides* species are needed to estimate size at sexual maturity, fecundity, and reproductive period and to determine locations that are favorable for spawning in order to better understand the life cycle of these species and, therefore, to improve fisheries management toward a more sustainable resource (Sparre and Venema, 1998; Chubb, 2000).

Chace (1967) reported that a population of the red slipper lobster (*S. herklotsii*) supported an intense fishing effort at Saint Helena (South Atlantic), and DeMartini and Williams (2001) noted that the blunt slipper lobster accounted for 64% of the lobster catch at Maro Reef (Northwestern Hawaiian Islands). Species of *Scyllaridae* also are targeted by other fisheries (e.g., in the Mediterranean Sea, Australia, the Galapagos Islands, India, and Australia); however, the numbers of fisheries landings from lobster catches have declined rapidly worldwide, and fisheries failures have occurred or are likely to occur in the near future (Lavalli and Spanier, 2007; Spanier and Lavalli, 2007). Studies show that generally in several places in the world most fisheries that have targeted slipper lobsters lacked effective regulations for the conservation of stocks and the economic maintenance of local fisheries (Lavalli and Spanier, 2007). A similar situation exists in Brazil, where there are no regulations that govern the extraction of these resources and where there is little specific knowledge about the basic biology of these species.

In Brazil, there are 3 genera of *Scyllaridae*: *Scyllarus*, *Parribacus*, and *Scyllarides*. Two species of *Scyllarides* occupy the south and southeast: 1) the Brazilian slipper lobster, distributed at depths of 20–130 m from Antilles to Brazil (Maranhão to São Paulo), and 2) the hooded slipper lobster, distributed at depths of 6–420 m from Argentina to Brazil (Rio de Janeiro to Rio Grande do Sul) (Holthuis, 1985, 1991; Melo, 1999; Oliveira et al., 2008; Duarte et al., 2010). Brazilian slipper lobsters are caught by 2 kinds of commercial fishing fleets in southeastern Brazil: 1) medium-size double trawlers that target mostly shrimp and 2) pot-and-trap fleets that target the common octopus (*Octopus vulgaris*). The lobsters caught by these fleets are traded intact (whole). Species of *Scyllarides* are not the main target of the majority of the fisheries off southeastern Brazil. In the same region, Duarte et al. (2010) have shown a significant reduction in the abundance of

the hooded slipper lobster despite a relatively low fishing effort. This reduction can be explained by its slow rate of population growth, high total mortality (Duarte et al., 2011), and late maturity (Oliveira et al., 2008) compared with other species of the same family. Also, traders have noted a smaller size of individuals in the catch in recent years (Duarte et al., 2011).

Brazil currently has no fishery management legislation that regulates the extraction of slipper lobsters in its waters, and data on the reproductive biology of these species of *Scyllaridae* would provide important life-cycle information that could be used for decision-making. Therefore, the aims of this study were to describe the relative growth (biometrics) and reproductive biology (maturity, reproductive period, fecundity, and spawning sites) of the hooded slipper lobster. We also sought to identify different population strata by sex, size, fishing area, and coloration of the carapace and to contribute the resulting data to inform future management recommendations that would promote sustainability and conservation of this species in commercial fisheries.

Materials and methods

Data collection on land

Weekly monitoring (through visits to landing sites) and 2 or 3 sampling efforts during the year were conducted for this study from May 2006 to April 2007 at all the industrial landing sites in the State of São Paulo, Brazil (at the sites of these 7 companies: 1) Cooperativa Mista de Pesca NIPO Brasileira, 2) Aliança, 3) Franzese, 4) Itafish, 5) Balãn, 6) TPPS-Santos, and 7) Araripe¹). About 70% of all the fishing landings that occurred in this study period were monitored, and, of the 100 fishing landings that were monitored, 72 landings were from medium-size double trawlers and 28 landings were from the pot-and-trap fleet (Instituto de Pesca, Governo do Estado de São Paulo, ProPesq, <http://www.pesca.sp.gov.br/estatistica.php>). As part of this monitoring, the total catch of hooded slipper lobster and information about the fishing areas (depth, latitude, and substrate type) were recorded.

The double trawler vessels have 2 identical semi-conical nets. The vertical opening of each net is created by a flotation device from a headrope 20.0 m in length, each mouth opening is 15.0 m wide by 1.5 m high, and trawl doors (weighing 60–80 kg) keep the net open. The majority of these vessels preserve their catch on board with ice (see illustrations in Duarte et al., 2010).

Fishing vessels that target common octopus have refrigerators for storage of their catch (Castanhari and Tomás, 2012). Each of these vessels can include up to

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

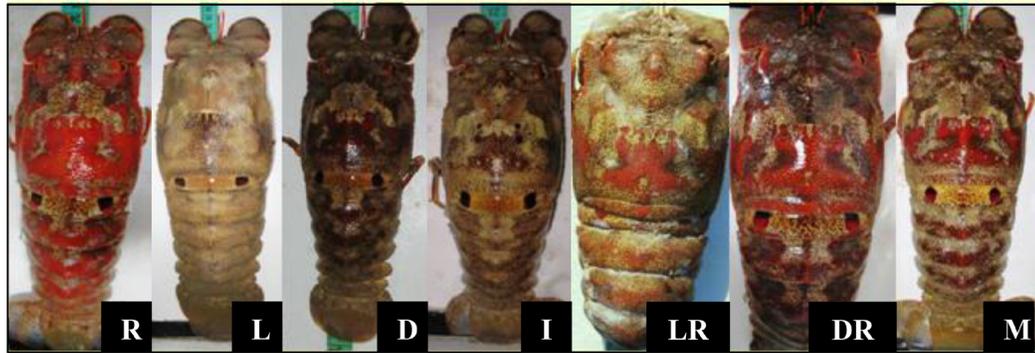


Figure 1

Carapace color patterns established for specimens of the hooded slipper lobster (*Scyllarides deceptor*) observed at fishery landings in southeastern Brazil from May 2006 to April 2007: red (R), light (L), dark (D), intermediate (I), light red (LR), dark red (DR), and mixed (M).

10 longlines with 2500 pots and 150 interspersed traps per longline, providing a total of 25,000 pots and 1500 traps for an individual fishery. The traps are baited (with remains of fishes) to catch octopuses, fishes, and slipper lobsters, and the pots are not baited, (Duarte et al., 2010; Castanhari and Tomás, 2012). Pots have a minimum internal diameter of 15 cm and are used as a shelter by common octopus. The number of pots cannot exceed 20,000 units per boat, and baited pots are not permitted with this type of fishing (SEAP, 2005) (see trap differences in Duarte et al., 2010). Lobsters are not caught in these pots.

Slipper lobster species were identified in this study by examination the morphological structure of the posterior margin of the 2nd abdominal pleura (Melo, 1999), which is a large concave spine in the hooded slipper lobster and straight or slightly convex in the Brazilian slipper lobster. Sex of lobsters was determined by the location of the gonopores on the base of the 3rd or 5th pair of pereopods in males and females, respectively (Abele, 1982; Hardwick and Cline, 1990).

Sampling efforts conducted at landing sites during the study period resulted in the collection of 1032 specimens, which were measured for biometric relationships and size structure with a tape measure attached to a wooden board for total length (TL), with a caliper for other linear measurements, and with a manual balance for the total weight (Abele, 1982). With a tape measure, TL was measured in centimeters from the distal tip of the antenna to the posterior end of the telson. The following measurements were obtained in millimeters with a caliper: carapace length (CL) between the distal extremity of the rostrum to the posterior margin of the carapace; carapace width (CW) between the sides of the carapace at its midpoint; abdomen width (AW) between the sides of the 1st and 2nd abdominal somites; abdomen length (LA) between the posterior margin of the carapace and the posterior end of the telson; and an-

tenna length (AL) from the base to the distal tip. The total weight (Wz) was measured in grams by weighing the intact, fresh animal.

The carapace color of each specimen was recorded upon landing and was classified according to 7 patterns (Fig. 1), 3 of which were established by the predominant color (>75%): red (R), light (L), and dark (D). The remaining 4 patterns were classified by their color tone. For 3 of the remaining patterns, ~50% of a carapace had to have an intermediate (I), light red (LR), or dark red (DR) tone; for the fourth pattern, ~33.3% of a carapace had to have a mixed (M) tone.

All the ovigerous females (100%, $n=22$) were recorded and collected during the sampling efforts from May 2006 to April 2007. During the study period, this subsample of 22 female specimens, with lengths that ranged from 22.5 to 32.0 cm TL, were collected from different boats, and their stage of embryonic development was categorized according to the classification of DeMartini and Williams (2001). The animals were placed in individual plastic bags and kept in crushed ice before laboratory analysis.

Laboratory processing

Females also were collected at the time of landing and were later dissected for macroscopic examination of their gonads, which were categorized according to the classification proposed by Stewart et al. (1997) and Haddy et al. (2005). This classification was established for lobster species from the genus *Ibacus* and is also valid for the species in our study because of identical macroscopic characteristics. Five maturation stages were established: the first 2 stages for juvenile individuals and stages 3–5 for mature individuals. At stage 1, the ovary is small, narrow, translucent to white, and has no visible oocytes. A female at stage 2 has a small and cream to yellow ovary with no visible oocytes. At

stage 3, the ovary is developed, has a small volume and is orange, and has visible oocytes at the ovary wall. At stage 4, the ovary is largely inflated, fills the whole carapace cavity, and is bright orange, with oocytes clearly visible along the ovary wall. Finally, at stage 5, the ovary is developed but has a flaccid appearance and is cream to yellow; there may still be some oocytes on the ovary wall—a specific peculiarity of this stage.

Individual fecundity was quantified volumetrically (Vazzoler, 1996) by using females with eggs in the early stages of embryonic development (orange in color). This method avoided underestimation caused with females at later stages, when there was the possibility of loss of eggs with catching and handling, or early larval hatching (DeMartini and Williams, 2001). The laboratory protocols were the same as those of Vazzoler (1996); eggs were removed from pleopods by dissociation in 10% NaClO, and were then vigorously stirred. The oocytes from each egg mass were transferred to a 1-L beaker and homogenized with a glass rod, and seven 5-mL subsamples were removed with a pipette. The oocytes were placed in gridded petri dishes for counting under a stereomicroscope (20×). We estimated individual fecundity (F) according to the method proposed by DeMartini and Williams (2001), counting the number of eggs in subsamples, discarding the extreme values (minimum and maximum), and calculating the mean individual fecundity of the 5 remaining subsamples (fs) with the following equation:

$$F = (tv \times fs) / dv, \quad (1)$$

where tv = total volume of the egg mass with a dilution of 1 L; and

dv = the dilution volume of the egg subsample or 5 mL).

The relationship of TL to the number of eggs (NE) was calculated with the following equation:

$$NE = (b \times TL) - a, \quad (2)$$

where a = the intercept; and

b = the slope of linear regression.

Data analysis

The statistical analyses for this study were performed with R software, vers. 2.13.0 (R Development Core Team, 2011) (Ihaka and Gentleman, 1996), and the fisheries were mapped with the Surfer contouring and 3-D mapping package, vers. 8 (Golden Software, Golden, CO). We adopted the TL as the size indicator for the hooded slipper lobster, as was done in previous studies of lobsters of the genus *Scyllarides* (Hearn, 2006; Pessani and Mura, 2007).

The relative growth of each sex was assessed by a regression analysis of the empirical points for morphometric relationships given by the power function $y=ax^b$, and then a t -test was used to check for possible differences in allometry (Huxley, 1950). The following

morphometric relationships were evaluated: AL×TL, CL×TL, LA×TL, AW×TL, CW×TL and W×TL (Abele, 1982). These relationships indicated the possible differences between the linear regressions obtained for each sex by comparisons with an analysis of covariance of constants a and b in the linear regressions of the biometric relationships (Zar, 1999; Faraway, 2002).

To represent the allometric relationships from the power function in a linear form, the dependent (y -axis) and independent (x -axis) variables were transformed by natural logarithms (ln). This transformation,

$$\ln y = \ln a + (b \times \ln x), \quad (3)$$

facilitates the use of a least squares fitting technique with linear regression:

$$y = a + (b \times x). \quad (4)$$

This mathematical procedure transforms the curvilinear relationship into a linear equation or equations and enables graphic comparisons of linear growth phases for the evaluation of biometric distinctions between developmental stages (juvenile and adult). Therefore, the linearized data ($\ln y = \ln a + [b \times \ln x]$) for each relationship were assessed with the segmented library (Muggeo, 2008) in R (vers. 2.13.0) to identify significantly different growth rates during ontogeny, according to procedures used by Pardal-Souza and Pinheiro (2012). This method of regression analysis seeks to partition the independent variable into intervals at break points, separating line segments that are fitted to each interval. The mean length at which 50% of females reached maturity (L_{50}) was estimated, under sigmoid adjustment, from the proportion of individuals with mature gonads (females in stages 3–5) in size classes of 1 cm TL (Hovgard and Lassen, 2000):

$$P = 1 / (1 + e^{-r(L - L_{50})}), \quad (5)$$

where P = the probability that a female is mature;

r = the slope;

L_{50} = the mean TL where the probability of mature females is 50%; and

L = the mean TL.

Data on the carapace color were analyzed in relation to size class, sex, the area of capture, and fishing gear. Five major fishing areas were established by mapping the fishing grounds of 2 types of vessels with different storage types (double trawlers that store their catch on ice and vessels that use pots and traps and store catch in refrigerators) on the basis of their similar latitudes and depths of fishing grounds for lobster species. Size composition and sex also were evaluated by fishing area, season, and month of capture. Size distribution was compared between sexes by using a t -test (Zar, 1999). An analysis of variance was used, separately for each variable, to evaluate the occurrence of different color patterns by sex (exclusivity or predominant patterns), fleet (differences in storage type), capture period (month and season), and fishing area, as well as to

Table 1

Morphometric relationships for the hooded slipper lobster (*Scyllarides deceptor*) sampled from May 2006 through April 2007 from pot-and-trap and double-trawler fleets that operate off southeastern Brazil. Data include results from mathematical equations (power function and log transformation), adjustments (coefficient of determination [r^2]), and analysis of covariance between the regressions of each biometric relation and allometric representation with 5% significance (t -test). AL=antenna length; LA=abdomen length; CL=carapace length; TL=total length; abdomen width=AW; CW=carapace width; W=weight; 0=isometric growth ($b=1$); +=positive allometric growth ($b>1$); -=negative allometric growth ($b<1$); M=males; and F=females. The relationship of the weight of animals was compared with the value 3 for b from the morphometric analysis. Significance codes: ns= $P>0.05$; *= $P<0.05$; **= $P<0.01$; and ***= $P<0.001$.

Morphometric relation	Sex	n	Power function $Y = ax^b$	Power function (linear form) $\ln y = \ln a + (b \times \ln x)$	r^2	Intercept (a)	Slope allometry (b)	($P<0.05$)
AL×TL	M	189	$AL=0.243 TL^{0.973}$	$\ln AL=-1.48+0.973 \ln TL$	0.85	0.021	0.111	0
	F	184	$AL=0.281 TL^{0.944}$	$\ln AL=-1.27+0.944 \ln TL$	0.92	*	ns	-
CL×TL	M	191	$CL=0.515 TL^{0.919}$	$\ln CL=-0.664+0.919 \ln TL$	0.92	0.006	0.626	-
	F	182	$CL=0.470 TL^{0.934}$	$\ln CL=-0.755+0.934 \ln TL$	0.97	**	ns	-
LA×TL	M	190	$AL=0.339 TL^{1.054}$	$\ln AL=-1.081+1.054 \ln TL$	0.89	0.0002	0.352	0
	F	184	$AL=0.321 TL^{1.068}$	$\ln AL=-1.14+1.067 \ln TL$	0.97	***	ns	+
AW×TL	M	163	$AW=0.312 TL^{0.951}$	$\ln AW=-1.16+0.951 \ln TL$	0.93	$<2.10^{-16}$	0.066	0
	F	171	$AW=0.269 TL^{0.986}$	$\ln AW=-1.31+0.986 \ln TL$	0.93	***	ns	0
CW×TL	M	272	$CW=0.653 TL^{0.869}$	$\ln CW=-0.427+0.869 \ln TL$	0.9	0.225	0.376	-
	F	266	$CW=0.657 TL^{0.868}$	$\ln CW=-0.419+0.868 \ln TL$	0.95	ns	ns	-
	Total	538	$CW=0.655 TL^{0.860}$	$\ln CW=-0.401+0.864 \ln TL$	0.94	-	-	-
W×TL	M	392	$W=0.0644 TL^{2.73}$	$\ln W=-9.037+2.73 \ln TL$	0.93	0.289	$<2.10^{-16}$	-
	F	437	$W=0.0771 TL^{2.67}$	$\ln W=-8.707+2.67 \ln TL$	0.93	ns	***	-

evaluate the size of the specimens by sex. Interactions between variables were not evaluated. In all cases, the means were compared by a posteriori multiple comparison with Tukey's honestly significant difference test (Zar, 1999; Faraway, 2002). The chi-square (χ^2) test was used to evaluate whether the sex ratio was different from 1:1 in samples with a sample size (n) ≥ 10 individuals (Zar, 1999), depending on the month, season, size class (TL, measured in centimeters), fishing gear, and fishing area.

Results

Distributions of fishing cruises and specimens caught

Of the 72 landings by 25 double trawlers that operated at depths of 40–220 m between the latitudes 23°20'S and 26°13'S during the study period from May 2006 to April 2007, 51.4% contained specimens of the hooded slipper lobster. Lobster occurred in 100% of the 28 landings of the pot-and-trap fleet, which operated at depths of 43–180 m and at latitudes between 23°30'S and 27°00'S.

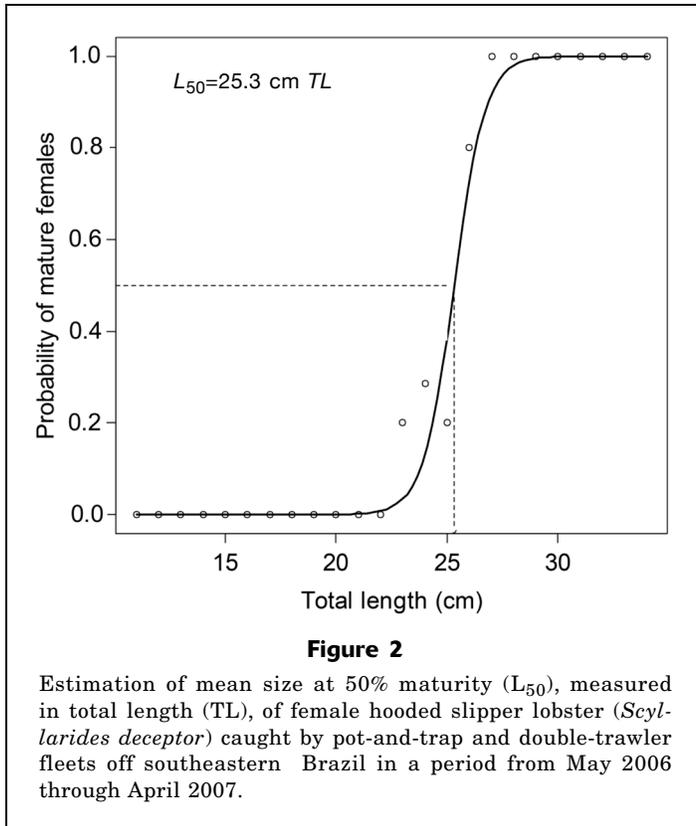
During the study period, 1029 specimens were counted, with most obtained by the pot-and-trap fleet (65.2%) rather than by double trawlers (34.8%). The hooded slipper lobster was abundant during all months of the study period. A small number of specimens of

the Brazilian slipper lobster were captured in April 2007 from a single double trawler landing from a depth between 45 and 130 m farther north in the study area (from 23°30'S, 43°00'W to 24°19'S, 45°09'W).

Relative growth

All the morphometric relations showed a coefficient of determination (r^2) with values between 0.85 and 0.97 (Table 1). The relation AL×TL (females), as well as the relations of CL×TL, CW×TL, and W×TL (both sexes), showed a negative allometry of the dependent variables in relation to body size (TL) of hooded slipper lobster. The allometric growth was positive only for the relation LA×TL (females) ($b>1$), indicating a higher growth rate of the dependent variable in relation to the body size of this sex. For other cases, the growth was isometric ($b=1$), indicating no change in growth rate between the variables during ontogeny. However, no inflection (or break point) was observed during the segmentation analysis of the regression lines, indicating no significant morphometric differences between juveniles and adults for both sexes of the hooded slipper lobster.

In the analysis of covariance (Table 1), the linear growth phases of juveniles and adults were observed to be similar between the sexes in the CW×TL linear equations and could be grouped for the total number of individuals of both sexes combined. This phenomenon was not observed for the other relationships (AL×TL,



CL×TL, LA×TL, and AW×TL), where statistically significant differences were detected between the indexes of origin a (intercept) but not between the values of b (slope), indicating mild sexual dimorphism. This analysis indicates that males had higher values of AL and CL than females for the same reference size (TL). The same was true for females, compared with males, with regard to LA and AW. However, the relationship W×TL differed significantly between the sexes for the value b in the linear regression, giving greater weight to larger males.

Reproduction

For this study, 49 female hooded slipper lobster (13.0–36.0 cm TL) were dissected, and their stages of gonad development were categorized. Of these females, 29 were classified as adults and 20 were classified as juveniles, resulting in an L_{50} of 25.3 cm TL (Fig. 2).

Only 22 ovigerous females were recorded in landings between May 2006 and April 2007 (pots and traps, $n=13$; double trawlers, $n=9$), corresponding to 11.2% of the 170 adult females caught and with sizes ranging from 22.5 to 32.0 cm TL. The spawning period occurred twice a year (Fig. 3), and a higher relative frequency occurred between July and October (60.5%) and a lower relative frequency, in January and February (7.2%).

Mean individual fecundities for 8 females (22.1–32.6 cm TL) ranged from 55,800 to 184,200 eggs. The linear relationship of number of eggs (NE) to TL (NE×TL) was

$$NE = (11,268 \times TL) - 183,361 \quad (n=8, r^2=0.82). \quad (6)$$

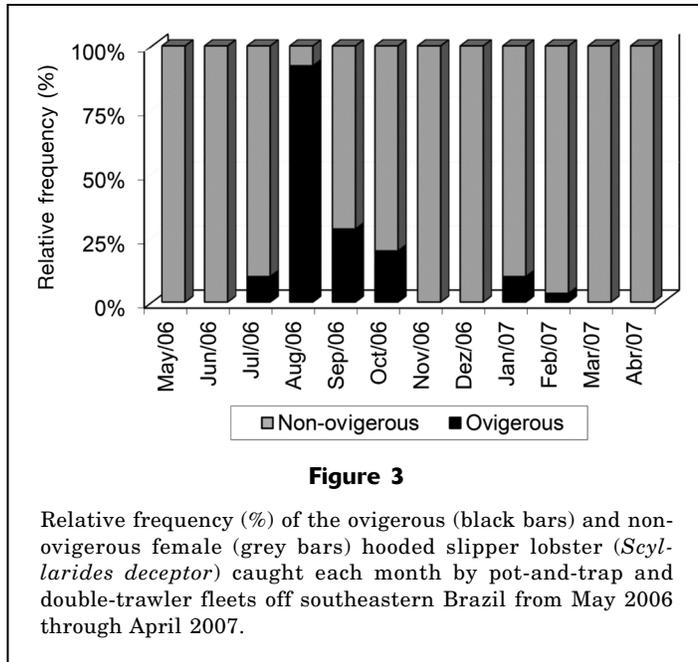
Size structure and sex ratio

The population structure of the hooded slipper lobster was very different among months as a function of TL, carapace color, fishing area, and season, both for males (Tukey's test: $3.69 \leq F \leq 9.03$; $P < 0.03$) and females (Tukey's test: $33.89 \leq F \leq 101.39$; $P < 0.03$). However, there were no changes in size composition (TL) as a function of fishing gear for both sexes ($P > 0.101$), where sizes ranged from 14.0 to 36.0 cm TL in the double-trawler fleet and from 11.0 to 36.0 cm TL in the pot-and-trap fleet. On the basis of analysis of their individual sizes, a high percentage of females were determined to be immature (double trawlers: 65.8%; pots and traps: 68.1%), and the monthly percentage of capture of immature females ranged from

Table 2

Depths of the 5 fishing areas of the double-trawler and pots-and-trap fleets that operate off southeastern Brazil and catch hooded slipper lobster (*Scyllarides deceptor*). Standard deviations (SD) of the means are provided in parentheses.

Fishing area	Depth (m)					
	Double trawlers			Pots and traps		
	Min.	Max.	Mean (SD)	Min.	Max.	Mean (SD)
Area 1	40	100	59.9 (16.8)	70	99	89.4 (10.2)
Area 2	40	80	58.3 (13.3)	43	100	79.2 (16.8)
Area 3	41	150	100.1 (38.2)	43	68	58.8 (12.3)
Area 4	100	165	134.5 (23.9)	100	180	120.0 (31.0)
Area 5	135	220	171.6 (44.0)	–	–	–
Total	40	220	91.1 (42.3)	43	180	81.4 (18.2)



40.5% (in December) to 83.3% (in November), independent of the fishing gear used, and higher levels were recorded in trawls (84.2%) during the spring and in pots and traps (72.6%) during the winter.

Size (TL) composition showed significant monthly variation, regardless of sex ($P < 0.001$), with greater differences between the monthly means for males (from 23.6 cm TL [standard deviation (SD) 3.4] in August to 19.6 cm TL [SD 2.8] in October) than for females (from 24.5 cm TL [SD 4.1] in May to 21.7 cm TL [SD 4.9] in November). No significant seasonal differences were observed in the size composition for each sex ($P = 0.14$) or in the sex ratio of hooded slipper lobster ($P > 0.05$). In general, the sex ratio of hooded slipper lobster (Table 3) did not differ significantly from a proportion of 1:1 ($P > 0.05$), regardless of the fishing gear used ($P = 0.85$). However, males predominated in smaller length classes (11.0–24.0 cm TL) and females in larger sizes (>24 cm TL). The t -test confirmed that females tended to be larger than males (males: 21.9 cm TL [SD 3.0]; females: 23.9 cm TL [SD 3.7]; $P < 0.001$).

The spatial distribution of the fishing areas for both fleets (areas 1–5; Fig. 4; Table 2) showed that the double-trawler fleet that caught Brazilian slipper lobster operated farther south (between the latitudes 25°00'S and 26°24'S) than the pot-and-trap fleet, at depths of 40–165 m, and particularly in areas 1 and 4. On the other hand, the pot-and-trap fleet concentrated fishing efforts in shallower waters (at depths of 43–100 m), between the latitudes 24°00'S and 25°00'S, and operated preferentially in area 2.

The males from area 5 were significantly smaller than those caught in areas 2 and 4 ($P < 0.01$) (Fig. 5). Females from area 5 also were smaller than females

caught in areas 3 and 4 ($P < 0.05$). The proportion of immature females among the adults caught in the trawl fleet ranged from 55% (area 4) to 90% (area 3), whereas, in the pot-and-trap fleet, the percentages of immature females were between 56.5% (area 2) and 75.9% (area 3).

In all fishing areas, males caught by double trawlers had a lower median size (20.7 cm TL) than males captured in pots or traps, and smaller individuals were observed in area 3. Females were more abundant in area 1 ($\chi^2: P = 0.036$), and males were more abundant in area 2 ($\chi^2: P = 0.01$).

Carapace color was used to classify 871 specimens of the hooded slipper lobster. The 7 categories evaluated were ranked in descending order (the absolute frequency for each category is shown in parentheses): D(259) > DR(247) > L(108) > R(103) > LR(91) > I(37) > M(26). The posteriori multiple comparison conducted with Tukey's test revealed significant differences between some of the color patterns for males (patterns: R≠L, I, and M; $P < 0.05$) and females (patterns: R≠L, I, LR, and M; $P < 0.001$). The R pattern showed the smallest variation (by size [TL]) and was characteristic of smaller individuals (mean: 21.5 cm TL [SD 2.7]), regardless of sex (Fig. 6). In addition, all females with this carapace color ($n = 8$, 27.6% of immature females) were identified by dissection as juveniles, and the other color patterns were found on both juveniles and adults. Therefore, an association between R pattern and a relatively narrow range of TLs was verified for both sexes. This relationship was not affected by the sex of the lobster, fleet composition (despite differences in storage of catch), month of capture, or fishing area.

Discussion

For the hooded slipper lobster, the r^2 values for morphometric relationships showed an excellent linear correlation. Females tended to show an increase in LA, therefore, enhancing their capacity for oviposition and for hatching a greater number of eggs in the bristles of their pleopods (individual fecundity) (Stewart et al., 1997; Demartini and Williams, 2001; Oliveira et al., 2008). Although the average female is larger than the average male, it is possible that an increase in body size (TL) in males facilitates the selection, grasping, and manipulation of females at the time of copulation, as has been observed in lobsters of the genus *Panulirus* (Lavalli and Spanier, 2007). Therefore, in general, significant differential growth was not observed between the juveniles and adults of each sex, nor was there obvious sexual dimorphism, although there was a small investment of energy in the width and length of the abdomen in females and in the carapace length for males in larger animals (>25 cm TL).

Various biometric equations presented high values of r^2 and thereby reinforced their suitability for use in

Table 3

Sex ratios (male:female) of the hooded slipper lobster (*Scyllarides deceptor*) by size classes (total length [TL]) caught by double-trawler and pot-and-trap fleets off southeastern Brazil from May 2006 through April 2007. Significance codes based on chi-square test (χ^2): ns= $P>0.05$; * $P<0.05$; ** $P<0.01$; and *** $P<0.001$.

Size classes (cm TL)	Number of specimens			Sex ratio (M:F)	P (χ^2)
	M	F	Total		
11–12	1	0	1	–	–
12–13	0	0	0	–	–
13–14	2	0	2	–	–
14–15	5	0	5	–	–
15–16	12	7	19	01:00.6	0.25 ns
16–17	14	14	28	01:01.0	1.00 ns
17–18	20	19	39	01:01.0	0.87 ns
18–19	37	14	51	01:00.4	0.0013***
19–20	53	26	79	01:00.5	0.0024***
20–21	71	33	104	01:00.5	0.0002***
21–22	62	58	120	01:00.9	0.53 ns
22–23	80	46	126	01:00.6	0.0025***
23–24	59	52	111	01:00.9	0.51 ns
24–25	41	71	112	01:01.7	0.0046*
25–26	18	53	71	01:02.9	0.0327*
26–27	12	42	54	01:03.5	0.0446*
27–28	11	25	36	01:02.3	0.0196*
28–29	7	16	23	01:02.3	0.0406*
29–30	5	11	16	01:02.2	0.13 ns
30–31	3	10	13	01:03.3	0.0522 ns
31–32	2	7	9	–	–
32–33	1	3	4	–	–
33–34	0	3	3	–	–
34–35	0	1	1	–	–
35–36	0	2	2	–	–

future interconversion between size variables, particularly measures of the abdomen (LA and AW) and individual body size (TL or CL). Currently, in Brazil, some boats have begun landing only the abdomen of lobsters (“headless” lobsters)—a trend that will hamper the use of CL for monitoring this resource in the future. Total length is measured routinely and is easier for fishermen to understand compared with the other measurements of size used in this study (Sparre and Venema, 1998; Chubb, 2000).

Values of L_{50} were smaller in species of the genera *Ibacus* (e.g., butterfly fan lobster) and *Thenus* (e.g., flathead lobster and *T. indicus*), with a species mean of 19.1 cm TL (SD 6.1) (Stewart et al., 1997; Courtney et al., 2001), compared with L_{50} values for species of the genus *Scyllarides* (e.g., blunt slipper lobster, Galapagos slipper lobster, and hooded slipper lobster), with a species mean of 25.0 cm TL (SD 5.6) (Demartini et al., 2005; Hearn and Toral-Granda, 2007; Oliveira et al., 2008). Oliveira et al. (2008) estimated that the L_{50} for female hooded slipper lobster was 25.1 cm TL—a

finding that is very similar to a result of our study ($L_{50}=25.3$ cm TL).

Oliveira et al. (2008) noted that copulation in the hooded slipper lobster occurs immediately after female molting—an aspect of the reproductive biology of this species that could not be assessed in this study because of the absence of molting or recently molted specimens. The absence of molting specimens in landings is most likely related to their reduced movement and the absence of feeding behavior at this stage (Lavalli and Spanier, 2007). These behaviors would preclude a molting lobster from entering a trap; therefore, fishery samples would not provide accurate copulation data.

This bias was not present in a study by Oliveira et al. (2008), who used data from monthly lobster population surveys conducted during diving expeditions at Santa Catarina Island (in southern Brazil), in June at the beginning of the molting and copulation season. Spanier et al. (1988) observed that the Mediterranean slipper lobster begins these biological processes during the same month in the southeastern Mediterranean,

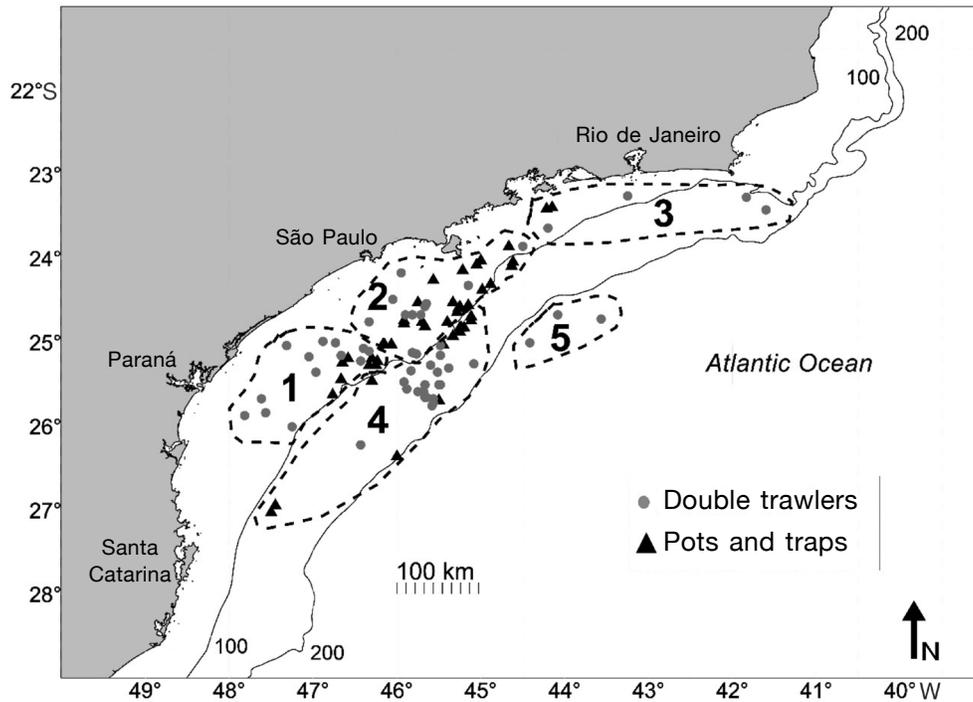


Figure 4

Spatial distribution of sampled effort of the double-trawler and pot-and-trap fleets that caught hooded slipper lobster (*Scyllarides deceptor*) off southeastern Brazil, within the established 5 fishing areas (outlined with dashed lines) from May 2006 through April 2007.

and Lavalli and Spanier (2007) mentioned the rapid calcification of the exoskeleton in species of this family, with the ovigerous condition occurring shortly thereafter. These observations agree with the finding from our study that the relative proportion of ovigerous females of the hooded slipper lobster is greater during August–September than in other periods and with the results of Oliveira et al. (2008).

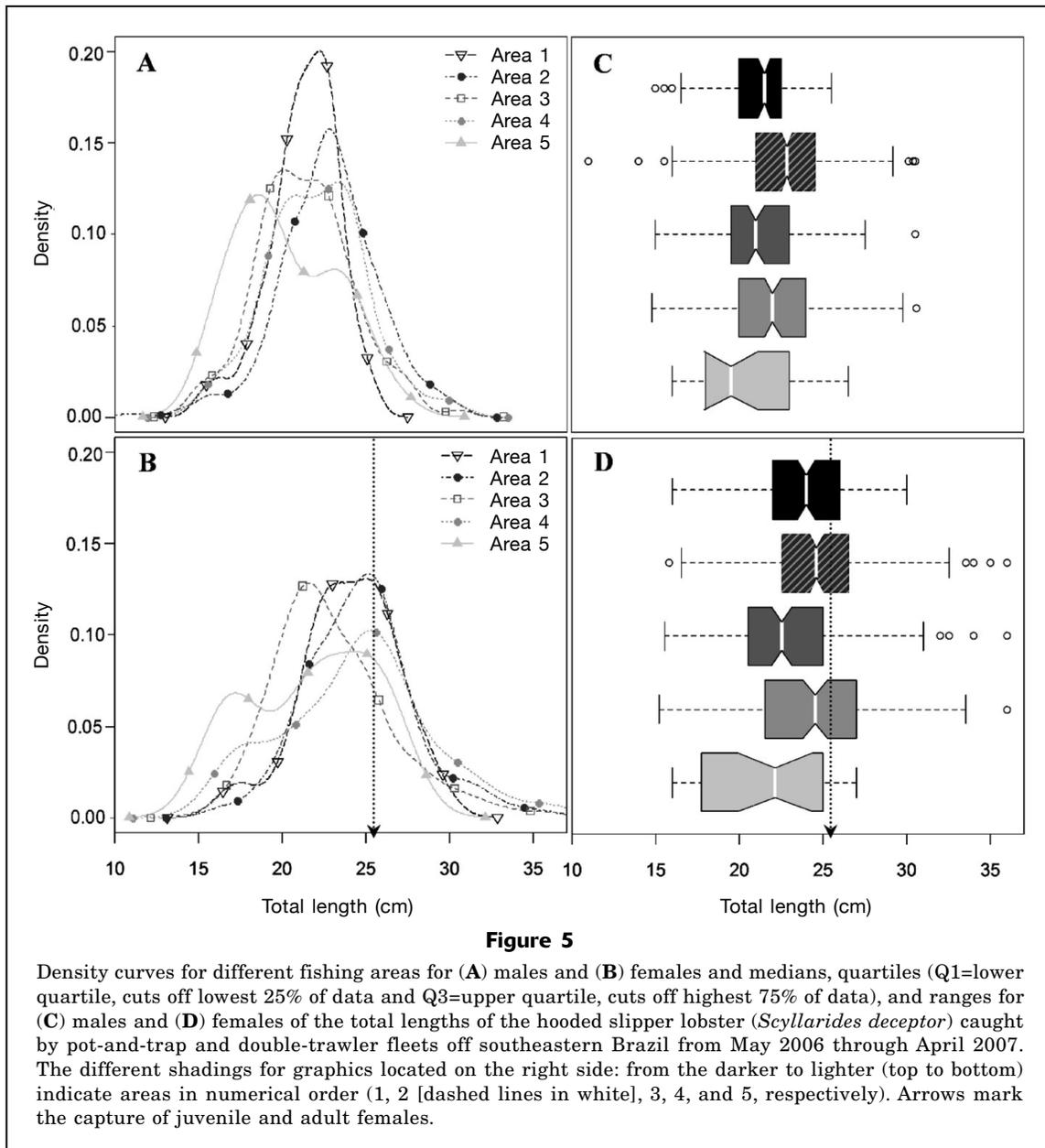
Another period in our study with a large proportion of ovigerous females occurred during January–February, indicating that there are 2 spawning seasons for the hooded slipper lobster. Lavalli and Spanier (2007) previously reported this spawning period for other *Scyllarides* species. Larvae released in September would experience a period of high primary production in the environment during October–March, when nutrients from the South Atlantic Central Water are present in shallower water (Rossi-Wongtschowski and Madureira, 2006). This reproductive strategy increases the probability of larval survival because complete larval development for *Scyllarides* spp. requires approximately 8 months (Booth et al., 2005).

The range of fecundity values and mean fecundity of hooded slipper lobster in this study were similar to those values reported for other species of the same genus (see review by Oliveira et al., 2008). According to these authors, hooded slipper lobster ($n=29$) had fecun-

dities between 58,871 and 517,675 eggs (mean=191,262 eggs (SD 17,811).

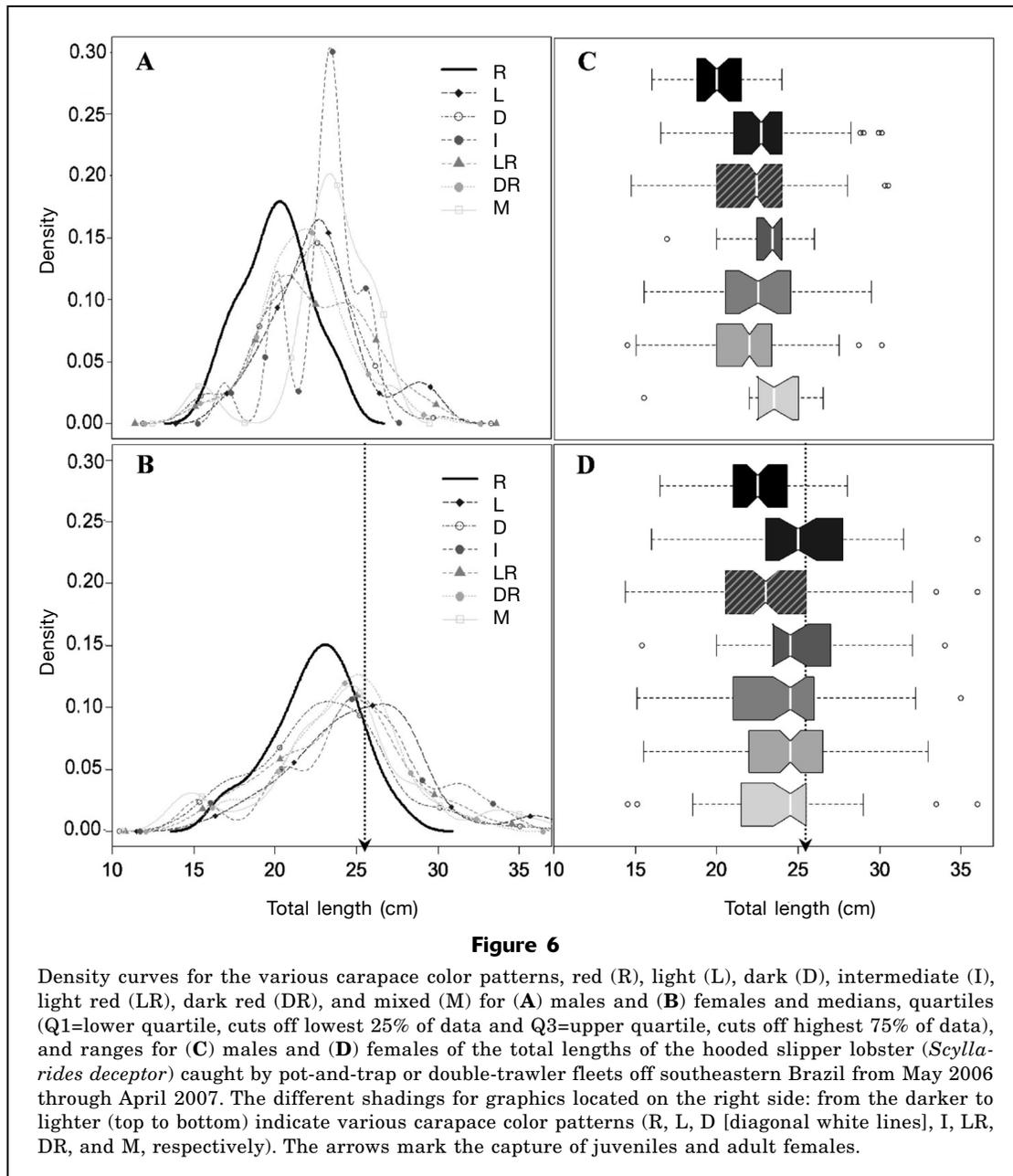
Research by Vazzoler (1996) suggested that the early maturity of a species lowers fecundity and increases oocyte size to preserve energy per egg and improve larval survival and reproductive success. This reproductive strategy is evident in Scyllaridae, as seen in the relationship between the mean sizes of lobster species and their gonadal maturation, fecundity, and egg diameter. According to Oliveira et al. (2008), the species of *Ibacus* and *Thenus* showed lower fecundity (13,000–21,000 eggs) and larger egg diameters (1.1–1.2 mm) than the fecundity (90,000–224,000 eggs) and egg diameters (0.60–0.67 mm) of species of *Scyllarides*. This observation reflects the reproductive strategy in Scyllaridae, which appears to differ depending on the bathymetric distribution of a given species. Species that are coastal, for example, tend to have lower fecundity and larger egg sizes (e.g., the flathead lobster and butterfly fan lobster, according to Courtney et al. [2001] and Stewart et al. [1997]) than species that inhabit deeper waters (e.g., the blunt slipper lobster, according DeMartini et al. [2005], and the hooded slipper lobster, as observed in this study).

Results from our study indicate that females of the hooded slipper lobster reach a larger size (maximum TL) than males (female: 36.0 cm TL; male: 32.6 cm TL),



in agreement with the results of Oliveira et al. (2008), who observed females that were 36.0 cm TL and males that were 31.0 cm TL. This characteristic is common in the Scyllaridae, but the opposite phenomenon occurs in the Palinuridae and Nephropidae (Spanier and Lavalli, 2007). In our study, the maximum sizes obtained were larger than the 32 cm TL reported by Holthuis (1991) and Spanier and Lavalli (2007). However, the hooded slipper lobster measured in our study were captured farther southeast in Brazil than were the hooded slipper lobster observed by Holthuis (1991) and Spanier and Lavalli (2007), and the lobster in our study were caught at maximum sizes that were similar to those of lobster found south of Brazil by Oliveira et al. (2008).

Those authors also identified 2 migration patterns for the hooded slipper lobster. One of them occurs daily and relates to foraging, and the other is seasonal for the hatching of larvae in shallower water. This latter migration pattern was confirmed in our study because only 4.5% of females were recorded at depths >100 m (area 4), and the remaining females were captured in shallow areas (mean depth <100 m): 27.3%, 63.6%, and 4.5% in areas 1, 2, and 3, respectively. According to information from fishermen in both fleets, each fishing area has the following typical substrate properties (granulometric predominance): area 1=sand, mud, and gravel (calcareous algae); area 2=mud and sand; area 3=sand and gravel; area 4=mud and sand; and



area 5=mud and sand. However, Figueiredo and Tesler (2004) report that the substrate varies greatly in microscale and therefore hampers association analyses.

In decapod crustaceans, carapace color patterns are a result of hormonal control of chromatotropines (Rao, 1985), combined with external factors, such as food sources, substrate color, and seasonal and environmental variations (Rao, 1985; Bedini, 2002). These patterns may also be associated with intrinsic biological factors, such as growth, reproduction, mating, and sexual maturation during ontogeny (Ryan, 1967; Pinheiro and Taddei, 2000). Analysis of the carapace color patterns

of the hooded slipper lobster in this study did not help to identify the reproductive period, timing of molting, or fishing areas for this lobster.

Chromatic changes during the ontogeny of crustaceans have been reported by Abele (1982) and Dalabona et al. (2005), particularly changes associated with maturation, as observed for other decapods of the genera *Callinectes* (Baldwin and Johnsen, 2012) and *Arenaeus* (Pinheiro and Taddei, 2000). In this study, there was a relationship between the size (TL) of females with red carapaces (range: 16.5–29.0 cm TL; mean; 22.7 cm TL [SD 2.9]) and L_{50} (25.3 cm TL), a size that was very

similar to the smallest ovigerous female registered in this study (22.5 cm TL). Therefore, it may be that the red chromatic pattern is related to maturation changes for this species, and this relationship should be evaluated in future experiments. The other coloration patterns were observed in lobster with a great range in size (TL) and were common to both sexes, possibly because color changes are more related to the time since molting, microscale substrate type, and trophic ecology of this species. There is a lack of specific studies concerning these influences, however.

For species of Scyllaridae, males are smaller than females (Lavalli and Spanier, 2007; Oliveira et al., 2008) and become mature at smaller sizes (e.g., *Ibacus* spp., according to Stewart et al., 1997). It is possible that red coloration may be used as an indicator of the chromatic changes in maturing males because the size distribution for this coloration was restricted to the range of 16.0 to 25.5 cm TL, with a mean of 20.4 cm TL (SD 2.7). On the basis of these results, it is likely that the L_{50} for males was approximately 23 cm TL, although more detailed analyses are required to confirm this hypothesis.

The reduction in stock sizes of hooded slipper lobster in our study area (see Duarte et al., 2010) presumably was enhanced by the capture of immature females (66.9%) with the 2 fishing methods: 1) trawlers and 2) pots and traps. On the basis of that observation, our research results indicate that the following potential measures could be investigated for the hooded slipper lobster fisheries in southeastern Brazil: 1) the use of a minimum landing size of 25 cm TL for this species, regardless of sex, and the release of individuals smaller than this size; 2) the release of ovigerous females immediately after capture to prevent an effect on recruitment; and 3) a closed season for fisheries from August to September, when there is the greatest reproductive activity (proportion of ovigerous females) for this species.

However, because discard mortality can be high in spiny lobsters (Gooding, 1985; O'Malley, 2008), whether discarding of hooded slipper lobster would be effective for stock protection is uncertain. Nevertheless, Castro et al. (2003) demonstrated the efficacy of releasing caught fish of the genus *Nephrops* as a management measure. Haddy et al. (2005) and Spanier and Lavalli (2006) suggested that slipper lobsters are more resistant to discard mortality, because of their thicker carapace (Melo, 1999), and usually return alive to the water. In addition, management actions, such as size limits, release of ovigerous females, and closed seasons were effective management controls for the *Panulirus cygnus* fishery (Hall and Chubb, 2001), indicating that such measures could be pertinent for slipper lobster fisheries.

In this study, we examined the life history aspects of the hooded slipper lobster landed as bycatch in 2 fisheries in Brazil. The biometry, reproductive status, and size structure were documented. Our main find-

ings were that maturity was related to the sizes of abdomen (females) and carapace (males); the ovigerous specimens occurred mainly in shallow waters, where fisheries were more intense; and higher numbers of juveniles than of adults were reported by fishing fleets with landings in the study area. In addition, it is possible that the red color of the carapace was related to maturation changes for this species. These results agree with evidence of fishing pressure on the slipper lobster population that was documented in other studies (Lavalli and Spanier, 2007; Spanier and Lavalli, 2007; Duarte et al., 2010).

Nevertheless, further studies are clearly still necessary, especially those that examine the life cycle and other parameters of the current populations of slipper lobsters in Brazil to understand mortality, growth, recruitment, stock identities, and stock levels of the hooded slipper lobster in waters of southeastern Brazil.

Acknowledgments

We thank all of the captains, fishermen, and dock workers at the various landings who contributed to this study. We also recognize the Instituto de Pesca (Santos, São Paulo), its Graduate Program in Fisheries and Aquaculture, and several colleagues for their input and help. We acknowledge the advice and help received from several colleagues, especially G. Pinheiro, who gave special attention to the figures in our manuscript. M. Pinheiro and M. Gasalla are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research fellowships provided. We also thank the reviewers who contributed much to improve this study.

Literature cited

- Abele, L. G. (ed.)
1982. The biology of Crustacea, vol. 2: embryology, morphology and genetics, 440 p. Dep. Biol. Sci., Florida State Univ., Tallahassee, FL.
- Baldwin, J., and S. Johnsen.
2012. The male blue crab, *Callinectes sapidus*, uses both chromatic and achromatic cues during mate choice. *J. Exp. Biol.* 215:1184–1191. doi: 10.1242/jeb.067512.
- Bedini, R.
2002. Colour change and mimicry from juvenile to adult: *Xantho poressa* (Olivi, 1792) (Brachyura, Xanthidae) and *Carcinus maenas* (Linnaeus, 1758) (Brachyura, Portunidae). *Crustaceana* 75:703–710. doi: 10.1163/156854002760202688.
- Booth, J. D., W. R. Webber, H. Sekiguchi, and E. Coutures.
2005. Review: diverse larval recruitment strategies within the Scyllaridae. *N.Z.J. Mar. Freshw. Res.* 39:581–592. doi: 10.1080/00288330.2005.9517337.
- Castanhari, G., and A. R. G. Tomás.
2012. Beak increment counts as a tool for growth studies of the common octopus *Octopus vulgaris* in southern Brazil. *Bol. Inst. Pesca* 38:323–331.

- Castro, M., A. Araújo, P. Monteiro, A. M. Madeira, and W. Silvert.
2003. The efficacy of releasing caught *Nephrops* as a management measure. *Fish. Res.* 65:475–484. doi: 10.1016/j.fishres.2003.09.033.
- Chubb, C. F.
2000. Reproductive biology: issues for management. In *Spiny lobsters: fisheries and culture*, 2nd ed. (B. F. Phillips and J. Kittaka, eds.), p. 245–275. Fishing News Books, Oxford, UK.
- Chace, F. A., Jr.
1967. Decapod crustaceans from St. Helena Island, South Atlantic. *Proc. U.S. Natl. Mus.* 118:623–661.
- Courtney, A. J., M. G. Cosgrove, and D. J. Die.
2001. Population dynamics of Scyllarid [sic.] lobsters of the genus *Thenus* spp. on the Queensland (Australia) East coast: I. assessing the effects of tagging. *Fish. Res.* 53:251–261. doi: 10.1016/S0165-7836(00)00274-5.
- Dalabona, G., J. L. Silva, and M. A. A. Pinheiro.
2005. Size at morphological maturity of *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae) in the Laranjeiras Bay, Southern Brazil. *Braz. Arch. Biol. Technol.* 48:139–145. doi: 10.1590/S1516-89132005000100018.
- DeMartini, E. E., M. L. McCracken, R. B. E. Moffitt, and J. A. Wetherall.
2005. Relative pleopod length as an indicator of size at sexual maturity in slipper (*Scyllarides squammosus*) and spiny Hawaiian (*Palinurus marginatus*) lobsters. *Fish. Bull.* 103:23–33.
- DeMartini, E. E. E., and H. A. Williams.
2001. Fecundity and egg size of *Scyllarides squammosus* (Decapoda: Scyllaridae) at Maro Reef, Northwestern Hawaiian Islands. *J. Crust. Biol.* 21:891–896. doi: 10.1651/0278-0372(2001)021[0891:FAESOS]2.0.CO;2.
- Duarte, L. F. A., E. Severino-Rodrigues, M. A. Gasalla.
2010. Slipper lobster (Crustacea, Decapoda, Scyllaridae) fisheries off the southeastern coast of Brazil: I. exploitation patterns between 23°00' and 29°65'S. *Fish. Res.* 102:141–151. doi: 10.1016/j.fishres.2009.11.004.
- Duarte, L. F. A., E. Severino-Rodrigues, M. A. Gasalla.
2011. Contextualização da pesca mundial de lagostas e características de comercialização de *Scyllarides* spp. e *Panulirus* spp. na Baixada Santista, Estado de São Paulo, Brasil. *Bol. Inst. Pesca.* 37:235–246.
- Faraway, J. J.
2002. Practical regression and Anova using R, 212 p. [Available from <http://cran.r-project.org/doc/contrib/Faraway-PRA.pdf>.]
- Figueiredo, A. G., Jr., and M. G. Tessler (eds.).
2004. Topografia e composição do substrato marinho da Região Sudeste-Sul do Brasil, 64 p. Série Documentos Revizee:Score Sul. Revizee Geological. Instituto Oceanográfico, Univ. de São Paulo, São Paulo, Brazil.
- Gooding, R. M.
1985. Predation on released spiny lobster, *Panulirus marginatus*, during tests in the Northwestern Hawaiian Islands. *Mar. Fish. Rev.* 47(1):27–35.
- Haddy, J. A., A. J. Courtney, and D. P. Roy.
2005. Aspects of the reproductive biology and growth of balmain bugs (*Ibacus* spp.) (Scyllaridae). *J. Crust. Biol.* 25:263–273. doi: 10.1651/C-2521.
- Hall, N., and C. Chubb.
2001. The status of the western rock lobster, *Panulirus cygnus*, fishery and the effectiveness of management controls in increasing the egg production of the stock. *Mar. Freshw. Res.* 52:1657–1667. doi: 10.1071/MF01211.
- Hardwick, C. W. Jr., and G. B. Cline.
1990. Reproductive status, sex ratios and morphometrics of the slipper lobster *Scyllarides nodifer* in the northeastern Gulf of Mexico. *Northeast Gulf Sci.* 11:131–136.
- Hearn, A.
2006. Life history of the slipper lobster *Scyllarides astori* Holthuis 1960, in the Galapagos Islands, Ecuador. *J. Exp. Mar. Biol. Ecol.* 328:87–97. doi: 10.1016/j.jembe.2005.06.021.
- Hearn, A., and M. V. Toral-Granda.
2007. Reproductive biology of the red spiny lobster, *Panulirus penicillatus* and the Galapagos slipper lobster, *Scyllarides astori* in the Galapagos Islands. *Crustaceana* 80:297–312. doi: 10.1163/156854007780162505.
- Holthuis, L. B.
1985. A revision of the family Scyllaridae (Crustacea: Decapoda: Macrura). I. Subfamily Ibacinae. *Zool. Verh.* 218:3–130.
1991. FAO species catalogue, vol. 13. Marine lobsters of the world. FAO Fish. Synop. 125, 292 p. FAO, Rome.
- Hovgård, H., and H. Lassen.
2000. Manual on estimation of selectivity for gillnet and longline gears in abundance surveys. FAO Fish. Tech. Pap. 397, 84 p. FAO, Rome.
- Huxley, J. S.
1950. Relative growth and form transformation. *Proc. R. Soc. Lond., B* 137:465–469. doi: 10.1098/rspb.1950.0055.
- Ihaka, R., and R. Gentleman.
1996. R: a language for data analysis and graphics. *J. Comput. Graph. Stat.* 5:299–314. doi: 10.1080/10618600.1996.10474713.
- Kagwade, P. V., and L. M. Kabli.
1996. Reproductive biology of the sand lobster *Thenus orientalis* (Lund) from Bombay waters. *Indian J. Fish.* 43:13–25.
- Lavalli, K. L., and E. Spanier.
2007. Introduction to the biology and fisheries of slipper lobsters. In *The biology and fisheries of the slipper lobster* (K. L. Lavalli and E. Spanier, eds.), p. 3–21. CRC Press, Taylor & Francis Group, Boca Raton, FL.
- Melo, G. A. S.
1999. Manual de identificação dos crustáceos Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea, 551 p. Editora Plêiade/FAPESP, Univ. São Paulo, Brazil.
- Mugge, V. M. R.
2008. Segmented: an R package to fit regression models with broken-line relationships. *R News* 8:20–25.
- Oliveira, G., A. S. Freire, and P. R. K. Bertuol.
2008. Reproductive biology of the slipper lobster *Scyllarides deceptor* (Decapoda: Scyllaridae) along the southern Brazilian coast. *J. Mar. Biol. Assoc. U. K.* 88:1433–1440. doi: 10.1017/S0025315408001963.
- O'Malley, J. M.
2008. Evaluations of tag retention and a device for releasing discarded Hawaiian spiny lobsters *Panulirus marginatus*. *N. Am. J. Fish. Manage.* 28:619–624. doi: 10.1577/M07-102.1.
- Pardal-Souza, A. L., and M. A. A. Pinheiro.
2012. Relative growth and reproduction in *Achelous spinicarpus* (Crustacea: Portunidae) on the south-east-

- ern continental shelf of Brazil. *J. Mar. Biol. Assoc. U.K.* 93:667–674. doi: [10.1017/S0025315412000318](https://doi.org/10.1017/S0025315412000318).
- Pessani, D., and M. Mura.
2007. The biology of the Mediterranean scyllarids. *In* The biology and fisheries of the slipper lobster, Crustacean Issues 17 (K. L. Lavalli and E. Spanier, eds.), p. 263–286. CRC Press, Taylor & Francis Group, Boca Raton, FL.
- Pinheiro, M. M. A., and F. G. Taddei.
2000. Chromatic alteration in *Arenaeus cribrarius* (Lamarck) (Crustacea, Portunidae): an indicator of sexual maturity. *Rev. Bras. Zool.* 17:945–951. doi: [10.1590/S0101-81752000000400006](https://doi.org/10.1590/S0101-81752000000400006).
- R Development Core Team.
2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from <http://www.R-project.org>, accessed September 2012.
- Rao, K. R.
1985. Pigmentary effectors. *In* The biology of Crustacea, vol. 9. Integument, pigments, and hormonal processes (D. E. Bliss, and L. H. Mantel, eds.), p. 395–462. Academic Press, Orlando, FL.
- Rossi-Wongtschowski, C. L. B., and L. S.-P. Madureira.
2006. O ambiente oceanográfico da plataforma continental e do talude na Região Sudeste-Sul do Brasil, 472 p. Univ. São Paulo, Brazil.
- Ryan, E. P.
1967. The morphometry of sexually mature instars in the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae). *In* Proceedings of the symposium on Crustacea, Part II; Erankulam, India, 12–15 January 1965 (N. K. Pillai, ed.), p. 716–723. *Mar. Biol. Assoc. India*, Mandapam Camp, India.
- SEAP (Secretaria Especial de Aquicultura e Pesca).
2005. Presidência da República, Instrução Normativa nº 3 de 26 de abril de 2005—Establish criteria and procedures for the ordering of operations related to the fishing of octopus (*Octopus* spp.) in marine waters under Brazilian jurisdiction. [In Portuguese.] (Available from http://www.editoramagister.com/doc_247849_INSTRU CAO_NORMATIVA_N_3_DE_26_DE_ABRIL_DE_2005.aspx.)
- Spanier, E., M. Tom, S. Pisanty, and G. Almog.
1988. Seasonality and shelter selection by the slipper lobster *Scyllarides latus* in the southeastern Mediterranean. *Mar. Ecol. Prog. Ser.* 42:247–255.
- Spanier, E., and K. L. Lavalli.
1998. Natural history of *Scyllarides latus* (Crustacea: Decapoda): a review of the contemporary biological knowledge of the Mediterranean slipper lobster. *J. Nat. Hist.* 32:1769–1786. doi: [10.1080/00222939800771281](https://doi.org/10.1080/00222939800771281).
- Spanier, E., and K. L. Lavalli.
2006. *Scyllarides* Species. *In* Lobsters: biology, management, aquaculture and fisheries. (B. F. Phillips, ed.), p. 462–496. Blackwell Publishing, Oxford, U.K.
- Spanier, E., and K. L. Lavalli.
2007. Slipper lobster fisheries—present status and future perspectives. *In* The biology and fisheries of the slipper lobster, Crustacean Issues 17 (K. L. Lavalli and E. Spanier, eds.), p. 377–391. CRC Press, Taylor & Francis Group, Boca Raton, FL.
- Sparre, P., and S. C. Venema (eds.).
1998. Introduction to tropical fish stock assessment. Part 1: manual. FAO Fish. Tech. Pap. 306/1, rev 2, 407 p. FAO, Rome.
- Stewart, J., and S. J. Kennelly.
1997. Fecundity and egg-size of the Balmain bug *Ibacus peronii* (Leach, 1815) (Decapoda, Scyllaridae) off the east coast of Australia. *Crustaceana* 70:191–197. doi: [10.1163/156854097X00825](https://doi.org/10.1163/156854097X00825).
- Stewart, J., S. J. Kennelly, and O. Hdegh-Guldreng.
1997. Size at sexual maturity and the reproductive biology of two species of scyllarid lobster from New South Wales and Victoria, Australia. *Crustaceana* 70:344–367. doi: [10.1163/156854097X00618](https://doi.org/10.1163/156854097X00618).
- Vazzoler, A. E. A. M.
1996. Biologia da reprodução de peixes teleósteos: teoria e prática, 169 p. Univ. Estadual Maringá, Brazil.
- Zar, J. H.
1999. Biostatistical analysis, 4th ed., 929 p. Prentice Hall, Upper Saddle River, NJ.