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Reproductive activity of the tropical arrow squid *Doryteuthis plei* around São Sebastião Island (SE Brazil) based on a 10-year fisheries monitoring



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ABSTRACT

Monthly samples of *Doryteuthis plei* were obtained from the small-scale hand-jigging fishery around São Sebastião Island (24° S), Brazil, across seven fishing seasons (November–April) during the period 2002–2012, with the aim of identifying the exploited population patterns with emphasis on the reproductive activity. In order to explore the process of development of reproductive organs, the size-at-maturity, and the spatial–temporal factors explaining maturation, an analysis of the sex-ratio, maturity, gonado-somatic index (GSI), concentration of spermatophores, biometric relationships, and two GAMLSS (Generalized Additive Model for Location Scale and Shape) was applied. *D. plei* recruited to local fisheries at around 161 mm mantle length (ML), males being, on average, 1.6 times larger than females. Females appeared more frequently during the first three months of the fishing season while males tended to be more frequent at the end of the season, confirming the existence of female post-spawning mortality. The presence of high proportions of mature squid was found throughout the fishing seasons for both sexes. The size-at-maturity was estimated at 143.3 mm ML in females, and 210 mm ML, in males. Both statistical models indicated robust non-linear correlation between gonad weight, biometric variables, and spatial–temporal factors ($p < 0.001$). Ovary weight mostly correlated with accessory glands weight, while testis weight correlated with ML. In both sexes, depth was found to be a significant variable explaining maturation, with higher gonads weight between 15 m and 20 m, and especially in the island's South and Southeastern areas. Statistical models also evidenced a significant peak of gonad weight in February and March, for females, and in March, for males. Inter-annual variation showed a peak of gonad weight in the fishing season 2011–2012. Overall, findings based on long-term monitoring should assist resource management (e.g. for seasonal, size, and spawning area protection) which seems potentially valuable for long-term sustainability of local fishing communities.

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1. Introduction

The loliginid squid *Doryteuthis plei* (Blainville, 1823) is a semelparous species, i.e. it breeds only once in a lifetime (Boyle and Rodhouse, 2005). The species comprises an important fishery resource off the southern and southeastern coast of Brazil (Perez et al., 2002, 2005; Gasalla et al., 2005; Rodrigues and Gasalla, 2008; Postuma and Gasalla, 2010; Gasalla et al., 2010). Its distribution ranges from the coast of Florida, USA (Hixon et al., 1980) to Rio Grande do Sul, Brazil (Perez et al., 2005), and in the southernmost portion its presence has been associated with the Brazil Current

(Haimovici and Perez, 1991) and with South Atlantic Central Waters (SACW) summer bottom intrusions (Martins et al., 2006).

In the South Brazil Bight (SBB) area (*sensu* Matsuura, 1989), the species is more abundant during the summer, with males often larger than females showing a polymodal size structure, in contrast to females that show unimodal size structure. *D. plei* appears to spawn throughout the year, more intensely in summer, when the fisheries seem to take advantage of the spawning concentrations (Perez et al., 2002; Rodrigues and Gasalla, 2008). In this regard, both artisanal (hand-jigging) and industrial (shrimp-trawling) fisheries have exploited the stock in the whole area (Perez, 2002; Gasalla et al., 2005; Postuma and Gasalla, 2010). Some differences on spatial patterns in size-at-maturity in respect to season, depth ranges, and inshore-offshore migration have been found along the region, converging that summer coastal spawning squid tend to mature at larger sizes than their offshore counterparts in winter (Perez et al., 2002; Rodrigues and Gasalla, 2008).

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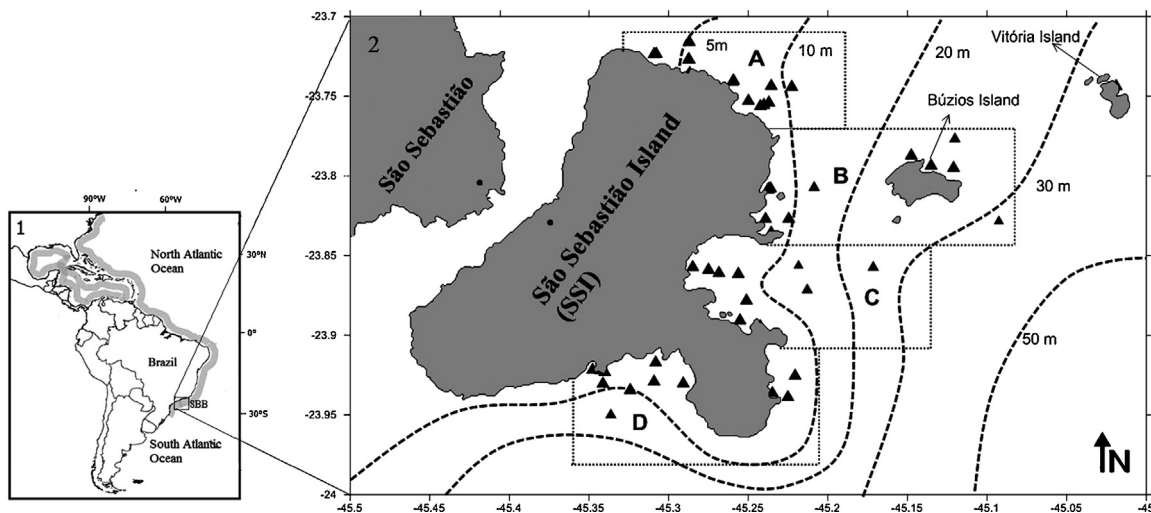


Fig. 1. Geographic distribution of the tropical arrow squid *Doryteuthis plei* (1) in the Western Atlantic Ocean (shaded area) and (2) in detail shows the area of operation of the small-scale squid hand-jigging fishery around São Sebastião Island (SSI) in the South Brazil Bight (SBB), the triangles representing the fishing spots in Latitude and Longitude. Depth ranges at 5, 10, 15, 20 and 30 m and the four fishing areas: (A) North, (B) Northeast, (C) Southeast and (D) South.

Overall, *D. plei* has been more studied on the shelf region (40–100 m deep) of the South Brazil Bight while little is known on their reproductive activity in coastal waters (<30 m), where the small-scale fisheries occurs. There are two main islands within the bight where squid hand-jigging has been reported: the Santa Catarina Island, at latitude 27.5° S (Martins and Perez, 2007), and the São Sebastião Island, at 24° S (Postuma and Gasalla, 2010). In the São Sebastião Island (SSI), squids have been caught especially in sheltered bays ~20 m deep and during both daylight hours and at night. The catch per unit effort (CPUE) tends to peak in the period from February to April, and the fisheries seems to operate under a wide range of environmental conditions, but especially in conditions of warm sea surface temperature, low wind and translucent waters, and just after summer rains (Postuma and Gasalla, 2010).

Previous studies on the reproductive activity of *D. plei* in Brazil have described spatial and seasonal patterns of maturity by using the gonado-somatic index (GSI) (Perez et al., 2002; Rodrigues and Gasalla, 2008), as has been occurring for other loliginids around the world (e.g., *Loligo vulgaris reynaudii* in South Africa, Olyott et al., 2006; *Loligo forbesi* in European waters, Porteiro and Martins, 1994; Guerra and Rocha, 1994; Rocha and Guerra, 1999; Pierce et al., 1994; Coelho et al., 1994; Pham et al., 2009; and *Doryteuthis sibogae* off the southeast coast of India, Neethiselvan et al., 2001). However, more recently, some generalized additive models (GAMs), based on the gonad weight, have been proposed to better understand the reproductive activity of certain European loliginid's stocks (e.g. Smith et al., 2005; Sanchez and Demestre, 2010), showing that more robust fits to data can be obtained to explain the main factors affecting reproduction, as one of the main advantages of the method.

Within this context, the main objective of the present study is to identify the exploited population patterns of *D. plei* around São Sebastião Island with emphasis on the reproductive activity monitored during a 10-year period, including the use of non-linear statistical models. Specifically, it is intended to explore the process of development of males and female reproductive organs, the main biometric variables that better translate the reproductive activity, the size at maturity, and the spatial and temporal factors that influence the reproduction of the species locally.

2. Materials and methods

2.1. Study area

São Sebastião Island (SSI) is located between 23°70' and 24°00' S and 45°50' and 45°00' W in the South Brazil Bight marine coast (Fig. 1). Small-scale hand-jigging fishery operates at a depth of between 5 and 30 m depth, mainly close to the shore and in the island's sheltered bays, but also close to smaller islands such as Búzios and Vitória (Fig. 1). The structure and dynamics of water masses occurring around SSI seem to be typical of the adjacent continental shelf, with a predominance of Coastal Waters (CW). Summer wind-driven bottom intrusions of the nutrient-rich South Atlantic Central Waters (SACW) seem to be the most relevant physical process for the ecosystem, promoting stratification of the water column and enhancing biological productivity (Castro et al., 2008; Pires-Vanin, 2008).

2.2. Squid sampling

During a 10-year period, samples were collected weekly from the landings of hand-jigging fishery operating around SSI, across seven fishing seasons (2002–03, 2003–04, 2004–05, 2006–07, 2008–09, 2010–2011 and 2011–2012) between November and April. All squid were caught at depths of less than 30 m. A total of 182 landings in the municipalities of São Sebastião (92%) and Ilhabela (8%) were monitored, from which 139 biological samples were collected, totalling 200 kg of squid. Information collected from the fishers included: fishing area (Fa), fishing depth (Fd) and fishing date, which allowed the identification of both fishing month (Fm) and fishing season (Fs).

2.3. Processing of samples

A total of 2351 specimens of *D. plei* caught by the small-scale hand-jigging fishery were sampled. The dorsal mantle length (ML) in mm and total body weight (BW) in g were recorded for each squid with an ichthyometer and a precision scale respectively. Squid dissection was conducted by cutting longitudinally the ventral size of the mantle to expose of the mantle cavity and visceral mass. The squid were sexed and the sexual maturity stage (I-immature,

Table 1
Number of specimens in the total sample and subsamples, for both sexes, obtained from fisheries landings across seven fishing seasons during the period 2002–2012.

Fishing season	Females		Males	
	Total Sample	Sub-sample	Total Sample	Sub-sample
2002–2003	148	0	119	0
2003–2004	143	0	170	0
2004–2005	188	28	117	28
2006–2007	206	44	113	70
2008–2009	182	141	149	149
2010–2011	211	141	205	164
2011–2012	211	182	189	101
Total	1289	536	1062	512

II-in maturation, III-mature and IV-spent) were determined macroscopically according to Juanicó (1983) and modified by Perez et al. (2002). Spermatophore concentration in the male Needham's sac was scored as (i) empty, (ii) few, (iii) many. Females were assessed for the presence (p) or absence (a) of spermatophores in the buccal receptacle (Roper, 1965; Porteiro and Martins, 1994). Table 1 summarizes the total sample and subsamples information during the fishing seasons that were investigated.

2.4. Reproductive structures

The following data were collected from reproductive organs: nidamental gland length (NiGL), oviducal gland length (OvGL), and accessory glands weight (nidamental + oviducal glands) (AGW), ovary (and proximal oviduct) weight (OW) of females; testis length (TL) and weight (TW), and spermatophoric complex weight (SW) (spermatophoric organ + Needham's sac) of males. The weight of the reproductive organs was measured to an accuracy of 0.001 g and their length to the nearest 0.1 mm (Perez et al., 2002; Porteiro and Martins, 1994; Rodrigues and Gasalla, 2008).

Based on previous CPUE analysis of the local fisheries (Postuma and Gasalla, 2003), the study area was divided in five depth strata (5 m, 10 m, 15 m, 20 m and 30 m) and four fishing areas: (A) North, (B) Northeast, (C) Southeast and (D) South (Fig. 1). The samples were grouped monthly and into the six months that comprise one fishing season (November–April) (Fs). A chi-square non-parametric test was used to determine significant differences between the sex-ratio among depth strata, fishing areas, and months; the null hypothesis (Ho) being the sex ratio 1:1, and the alternative hypothesis (Ha) the ratio being different from the parity.

ML–BW relationships were fitted using the power model ($ML = aBW^b$). The ML and BW were log-transformed and subsequently tested with covariance analysis ANCOVA to investigate the effect of the sex and maturity stages on the exponent “b” of the ML–BW relationship, where log BW was the dependent variable, sex and maturity stages, the factors of ANCOVA, and log ML, the covariable exponent (Zar, 1996). Squids at stages III and IV were pooled in the analysis because of the low frequency of spent squid in the samples. Initially, the gonado-somatic index (GSI), being defined as $GSI = 100 \times (OW + AGW) / BW$ for females, and $GSI = 100 \times (TW + SW) / BW$, in males, was used to observe spatial and temporal variations on reproductive activity. Both GSIs for males and females were tested for normality using a Shapiro–Wilk test. Because data were found to violate the criteria for normality, the non-parametric Kruskal–Wallis test (Hollander and Wolfe, 1973; Zar, 1996) was applied to test the influence of fisheries-related factors (i.e. area, month, and depth) on GSI. A post hoc pairwise comparison test was applied to determine which factor was significantly different from the average (Siegel and Castellan,

1988). All statistical tests were considered at a 0.05 level of significance.

The size at maturity (ML50) was estimated by fitting a sigmoid model $P = 1 / (1 + \exp(a + b \times ML))$, where variable P is the relative frequency of mature individuals at each ML class, a and b are parameters, and ML is the mantle length of mature squid. ML50 was estimated as being a/b of the fitted model.

2.5. Generalized additive models

GAMLSS were implemented using a series of packages in R (R Development Core Team, 2013) downloaded from <http://www.gamlss.org>. The GAMLSS procedure was used with a cubic spline smoothing function (cs) (Stasinopoulos and Rigby, 2007). Models were applied to analyze the correlations between body measurements and reproductive structures and with the spatial and temporal factors of the small-scale fisheries. Thus, two models were analyzed separately: the first one considering reproductive and biometric variables, and the second exploring the factors that better explain maturation expressed by gonad weight in terms of fisheries-related variables such as depth, area, month, and fishing season. The data were analyzed separately for males and females. The first model was defined: $OW \sim ML + BW + AGW + OvGL + NiGL + Mat$, for females, where Mat is the factor maturity stages, and $TW \sim ML + BW + SW + TL + Mat$, for males.

Moreover, the second model was used to determine the level of significance of the response variables (OW) and (TW) with the spatial (fishing area [Fa] and fishing depth [Fd]) and temporal (fishing month [Fm] and fishing season [Fs]) factors of the fisheries variability. Thus, the model used was: $(OW/TW) \sim Fd + Fa + Fm + Fs$.

For both models, a weibull's probability distribution was selected for the examination of the response variable for males, and a normal probability distribution for females. In both cases, a logarithmic function was used to link the mean distribution of the variable with the linear model. The variance inflator factor (VIF) was used to test co-linearity between variables in the GAMLSS (Montgomery and Peck, 1992). VIF values greater than 3 indicated collinearity, following the recommendation made by Zuur et al. (2010).

The best fitted models were selected based on the Akaike Information Criterion (AIC), Schwarz's Bayesian criterion (SBC) and Global Deviation (GD). The significance of each term was assessed using the “drop1” function, and their relative importance assessed accordingly to the AIC, likelihood-ratio test (LRT) and probability of the Chi-squared test criteria (PrChi) obtained (Stasinopoulos and Rigby, 2007).

3. Results

3.1. Population structure of squid *D. plei* caught by the São Sebastião Island small-scale fishery

From the total of 2351 *D. plei* specimens sampled, 1289 were females and 1062 males. Females were more frequent than males at depths ranging from 5 m to 10 m, in the South and Southeast areas, and mainly during the first three months of the fishing season (November, December, and January) where statistical difference was found significant (Table 2). The mean ML for females was 136.86 mm ML (± 34.17 s.d.; range: 30–231 mm), while in males it was 198.05 mm ML (± 62.46 s.d.; range: 49–390 mm). Females showed a unimodal distribution peaking at 140 mm ML, while males showed a multi-modal distribution (modes at 190 mm and 230 mm). Regarding the distribution of BW in specimens of *D. plei*, females tended to peak around 50 g, reaching a maximum of 162 g,

Table 2
Statistical analysis (χ^2) chi-square of differences between the sex ratio, depth, month and area. Differences between values were significant $\chi^2 > 3.48$ with 95% confidence ($p < 0.05$).

Variables	Factors	Females	Males	χ^2	P value
Depth (in meters)	5	294	178	28.50	<0.05
	10	593	511	6.09	<0.05
	15	242	231	0.25	0.61
	20	98	74	3.34	0.06
	30	8	5	0.69	0.4
Fishing month	November	355	193	47.90	<0.05
	December	121	102	1.61	<0.05
	January	273	210	8.21	<0.05
	February	297	276	0.76	0.38
	March	135	158	1.80	0.17
	April	96	100	0.88	0.77
Fishing area	North	496	428	5.00	0.025
	Northeast	142	148	0.12	0.724
	Southeast	299	228	9.56	<0.05
	South	352	258	14.50	<0.05
	Total		1289	1062	

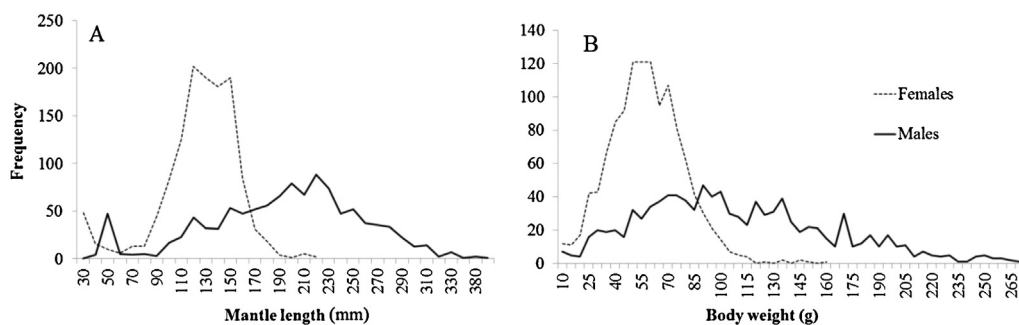


Fig. 2. The frequency of individuals (A) per mantle length (mm) class and (B) body weight (g) for males and females of *Doryteuthis plei* caught by the hand-jigging fishery around São Sebastião Island between 2002 and 2012.

while males peaked around 90 g, reaching a maximum of 297 g (Fig. 2).

The relationship between the ML/BW was obtained by non-linear fits (power function), as being $BW = 0.0021ML^{2.06}$ ($r^2 = 0.87$; $n = 1283$) and $BW = 0.0049ML^{1.86}$ ($r^2 = 0.86$; $n = 1056$), respectively for females and males. The exponent “b” values were significantly higher in females than in males (Fig. 3), and in immature and in-maturation individuals of both sexes, suggesting somatic growth

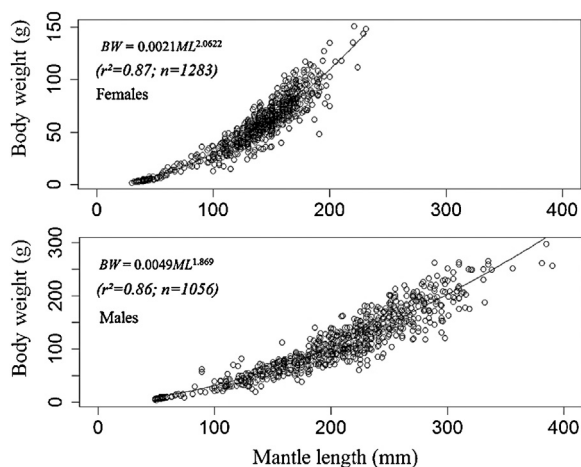


Fig. 3. ML/weight relationships for (A) females and (B) males of *Doryteuthis plei* caught by the small-scale squid hand-jigging fishery around São Sebastião Island (SSI) (24° S) during the period November–April 2012.

during these stages. The lower value in mature and spent (stages III and IV) suggests reproductive growth (Tables 3 and 4).

3.2. Reproductive activity

3.2.1. Females

Approximately 69% of the females were mature (stages III and IV) with a peak of maturity observed in February (Table 5). Both proportions of mature females and females with the presence of spermatophores in the buccal receptacle were present in all samples with the highest frequencies found at 10 m depth and in the fishing area Northeast (Table 5). The ML50 of squid caught by the local squid fishery was estimated at 143.3 mm (Fig. 4). The sum of the ovary weight + oviducal and nidamental glands represented a mean of 12.23% of total body weight with a range between 3.71 and 34.52%. The mean GSI was significantly different among areas (Kruskal–Wallis test, $p < 0.05$). The pairwise comparison test showed that the mean GSI was significantly higher in the south and southeast areas (Table 5) in relation to the others ($p < 0.05$).

In the first GAMLSS model for females, the residuals appear random, although the normal Q–Q plot shows a possible single outlier in the upper tail and a slightly longer extreme lower tail than the Box–Cox t -distribution. However, all GAMLSS models showed a good fit to the data.

Considering the biometric relationships, Table 6 shows the best-fitted GAMLSS model indicating that ML was the most significant explanatory variable according to the AIC criterion. A partial plot of such model showed a positive relationship with OW from 131 mm ML onward, peaking at 151 mm ML, with a slight decrease from 175 mm on (Fig. 5A). During maturation, the accessory gland weight

Table 3

Coefficients of the model fitted to the mantle length–weight relationship, $BW = aML^b$, of males and females of *Doryteuthis plei* for maturity and sex. The parameters a and b were estimated after the log linearization of ML and BW.

Maturity scale	Females			Males			
	a	b	r	a	b	r	r
(I) Immature	0.0009	2.27	0.95	0.0016	2.06	0.95	0.95
(II) In maturation	0.0054	1.85	0.85	0.0023	2.02	0.96	0.96
(III) Matures + (IV) spent	0.0049	1.88	0.86	0.0051	1.86	0.84	0.84

Table 4

Results of the covariance analysis ANCOVA to test the effect of sex and maturity (factors) on body weight (dependent variable) of female and male *Doryteuthis plei*, using ML as a covariate d.f.: degrees of freedom; MS: mean square. All variables were log transformed. The effect of the interaction between the factors and the covariate (maturity stage \times log ML) was used to test the exponent “ b ”.

Factors	df	MS	F	p
Log ML	1	234.550	37123.50	<0.001
Sex	1	0.451	71.41	<0.001
Sex \times log ML	1	0.562	88.96	<0.001
Males				
Log ML	1	75.191	8996.171	<0.001
Scale maturity	2	0.091	10.945	<0.001
Scale maturity \times log ML	2	0.092	11.057	<0.001
Females				
Log ML	1	32.443	5636.569	<0.001
Scale maturity	2	0.135	23.502	<0.001
Scale maturity \times log ML	2	0.117	20.416	<0.001

(AGW) showed a high correlation with OW, increasing monotonically (LRT and Chi-squared test in Table 6 and Fig. 5B). The NiGL also correlated positively to OW, increasing monotonically, with an inflection point at 31.5 mm (Fig. 5C). The OW increases significantly with maturity (Mat), showing a negative relationship with immature and in maturation squid, peaking in mature squids and decreasing slightly in spent (Fig. 5D).

In the second GAMLSS model, fishing depth (Fd) was the most important variable explaining the maturity in females (Table 7). The partial plot showed a positive correlation with OW between 15 m and 23 m, with a peak at depth of 20 m (Fig. 5E), and in the Southeast fishing area (Fig. 5F). The OW was positively correlated to the months February and March, while was negatively in other months (Fig. 5G). The inter-annual variation of OW also proved to be significant (LRT in Table 7), with positive correlation in the fishing season 2011–2012 (Fig. 5H).

3.2.2. Males

A high percentage of mature males (82%) were observed toward the end of all fishing seasons (February–March). Mature males

occurred more frequently in the Northeast fishing area, and also at 10 m depth, decreasing occurrence stepwise until 30 m (Table 5). The ML50 of males was estimated at 210 mm (Fig. 4). The spermatophoric complex (SW) represented on average 1.66% of body weight, ranging from 0.38% to 7.82%. The mean GSI was significantly different between areas (Fa) and months (Fm) (Kruskal–Wallis test, $p < 0.001$). The pairwise comparison test shows that the mean GSI was significantly higher in the Southern fishing area (Table 5). During March, mean GSI was significantly lower compared with other months ($p < 0.05$).

The first GAMLSS model for males indicated co-linearity between TW and BW (VIF = 3.05), so BW was excluded from the analysis. The best fitted model is shown in Table 6, being the spermatophoric complex weight (SW), the most significant explanatory variable, with high correlation during maturation, and increasing monotonically with TW (Fig. 6B). On the other hand, the ML was the most likely variable in the model (LRT and Chi-squared test, Table 7). The partial plot showed a positive correlation between TW and ML at 187.77 mm ML with a second peak at 281.01 mm ML (Fig. 6A). It also showed a positive relationship between TW and

Table 5

Mean of gonado-somatic index (GSI), percentage of mature individuals (% Mat), presence of spermatophores in the buccal membrane in females and concentration of spermatophore in Needham's sac in males (% Sperm) of *Doryteuthis plei* caught by the small-scale squid hand-jigging fishery around São Sebastião Island (SSI) during the period November 2002–April 2012.

Variables	Factors	Females			Males		
		Mean GSI	% Mat.	% Sperm.	Mean GSI	% Mat.	% Sperm.
Depth in (m)	5	12.36	25.61	24.65	1.59	17.81	17.80
	10	11.86	41.09	42.09	1.65	45.55	46.13
	15	12.45	20.71	20.69	1.62	23.63	22.77
	20	13.13	8.13	7.40	1.86	7.08	7.51
	30	11.92	4.45	5.17	1.93	5.94	5.20
Fishing month	November	12.53	27.56	24.16	1.72	12.79	13.76
	December	12.97	13.92	8.73	1.85	10.27	10.17
	January	11.77	26.99	22.94	1.80	21.12	20.12
	February	11.63	31.96	24.97	1.74	26.48	26.47
	March	12.35	16.05	11.17	1.41 ^a	17.24	17.23
Fishing area	April	12.98	11.08	8.02	1.58	12.10	12.25
	North	11.67	11.58	12.58	1.71	15.07	15.14
	Northeast	8.93	33.74	31.74	1.51	37.21	36.99
	Southeast	12.82 ^a	26.50	25.25	1.73 ^a	25.00	25.09
	South	13.34 ^a	28.17	30.43	1.89 ^a	22.72	22.77

^a Significant difference ($p < 0.05$), Kruskal–Wallis test.

Table 6
Summary of optimal GAMLSS models fitted to the ovary weight (OW) where explanatory variables are mantle length (ML), body weight (BW), accessory glands weight (AGW), oviducal gland length (OvGL), maturity (Mat) and nidamental gland length (NiGL) in females, while in males, testis weight (TW) and explanatory variables are spermatophoric complex weight (SW) and testis length (TL) from *Doryteuthis plei* caught by the small-scale squid hand-jigging fishery around São Sebastião Island (SSI) during the period November 2004–April 2012. (AIC = Akaike Information Criterion; LRT = Likelihood-ratio test; p(Chi) = probability of Chi squared test, and cs() = cubic spline).

Selected model (females): cs(OW) ~ cs(ML) + cs(BW) + cs(NiGL) + cs(AGW) + Mat								
Variables	Estimate	Std. Error	t value	Pr(> t)	AIC	LRT	Pr(Chi)	
(Intercept)	-0.108	0.146	-0.739	4.602e ⁻⁰¹				
ML (df=4)	0.001	0.001	-0.334	7.385e ⁻⁰¹	1711.67	5.25	0.386	
BW (df=4)	0.007	0.001	5.084	5.219e ⁻⁰⁷	1734.55	28.14	3.421e ⁻⁰⁵	
NiGL (df=4)	0.018	0.004	4.946	1.032e ⁻⁰⁶	1733.72	27.30	4.98e ⁻⁰⁵	
AGW (df=6)	0.158	0.012	13.413	2.635e ⁻³⁵	1836.85	134.44	7.431e ⁻²⁶	
Factors								
Mat in maturation	0.176	0.100	1.756	7.973e ⁻⁰²	1743.71	33.30	2.778e ⁻⁰⁷	
mature	0.340	0.098	3.448	6.117e ⁻⁰⁴				
spent	0.111	0.125	0.885	3.764e ⁻⁰¹				
Selected model (males): cs(TW) ~ cs(ML) + cs(SW) + cs(TL) + Mat								
(Intercept)	-2.061	0.104	-19.77	1.99e ⁻⁶⁴				
ML (df=4)	0.003	0.000	6.914	1.47e ⁻¹¹	456.37	66.46	7.646e ⁻¹²	
SW (df=6)	0.171	0.045	3.762	1.89e ⁻⁰⁴	416.71	22.79	0.0003	
TL (df=4)	0.016	0.002	7.697	7.73e ⁻¹⁴	441.26	47.35	4.816e ⁻⁰⁹	
Factors								
Mat in maturation	0.291	0.111	2.63	8.80e ⁻⁰³	417.47	19.55	0.0002	
mature	0.506	0.105	4.839	1.75e ⁻⁰⁶				
spent	0.481	0.131	3.685	2.54e ⁻⁰⁴				

Table 7
Summary of optimal GAMLSS models fitted to the weight of the ovary weight (OW) and testis weights (TW) of the *Doryteuthis plei*, and the explanatory variable with the spatial (fishing area [Fa], fishing depth [Fd], temporal (fishing months [Fm] and the fishing season [Fs]) of the small-scale squid hand-jigging fishery around São Sebastião Island (SSI) during the period November 2004–April 2012, where AIC = Akaike Information Criterion; LRT = Likelihood-ratio test; p(Chi) = probability of Chi squared test; and cs() = cubic spline.

Selected model (females): OW ~ cs(Fd) + Fa + Fm + Fs								
Variables	Factors	Estimate	Std. error	t Value	Pr(> t)	AIC	LRT	Pr(Chi)
(Intercept)		0.449	0.125	8.421	3.44e ⁻⁰⁴			
Fd	Fd (df=4)	0.009	0.094	1.928	5.44e ⁻⁰²	2125.67	15.28	0.009
Fa	Northeast	0.020	0.120	0.169	8.66e ⁻⁰¹	2142.33	27.94	3.73e ⁻⁰⁶
	South	0.790	0.057	2.153	3.71e ⁻¹⁶			
	Southeast	0.314	0.056	5.615	3.21e ⁻⁰⁸			
Fm	December	0.166	0.079	2.090	3.71e ⁻⁰²	2143.06	32.67	4.37e ⁻⁰⁶
	January	0.217	0.071	3.053	2.38e ⁻⁰³			
	February	0.301	0.068	4.452	1.04e ⁻⁰⁵			
	March	0.449	0.076	5.873	7.67e ⁻⁰⁹			
	April	0.243	0.080	3.049	2.42e ⁻⁰³			
Fs	2006–2007	0.328	0.112	2.939	3.44e ⁻⁰³	2236.51	124.12	7.02e ⁻²⁶
	2008–2009	0.423	0.098	4.326	1.83e ⁻⁰⁵			
	2011–2012	0.231	0.093	2.470	1.38e ⁻⁰²			
	2010–2011	0.122	0.004	3.604	3.18e ⁻⁰²			
Selected model (males): TW ~ cs(Fd) + Fa + Fm + Fs								
(Intercept)		-0.638	0.125	-5.103	4.78e ⁻⁰⁷			
Fd	Fd (df=4)	0.004	0.005	0.740	4.60e ⁻⁰¹	651.91	7.90	0.094
Fa	Northeast	0.179	0.078	2.295	2.22e ⁻⁰²	655.47	9.44	0.023
	South	0.081	0.055	1.469	1.42e ⁻⁰¹			
	Southeast	0.136	0.060	8.413	4.34e ⁻¹⁶			
Fm	December	-0.001	0.088	-0.011	9.92e ⁻⁰¹	676.17	34.15	2.22e ⁻⁰⁶
	January	0.787	0.094	6.608	5.44e ⁻⁰¹			
	February	-0.001	0.080	-0.008	9.93e ⁻⁰¹			
	March	0.291	0.077	3.793	1.67e ⁻⁰⁴			
	April	0.117	0.083	1.401	1.62e ⁻⁰¹			
Fs	2006–2007	0.493	0.094	5.231	2.50e ⁻⁰⁷	711.87	67.85	6.45e ⁻¹⁴
	2008–2009	0.726	0.094	7.713	6.81e ⁻¹⁴			
	2011–2012	0.503	0.092	5.447	8.09e ⁻⁰⁸			
	2010–2011	0.051	0.084	2.272	2.35e ⁻⁰²			

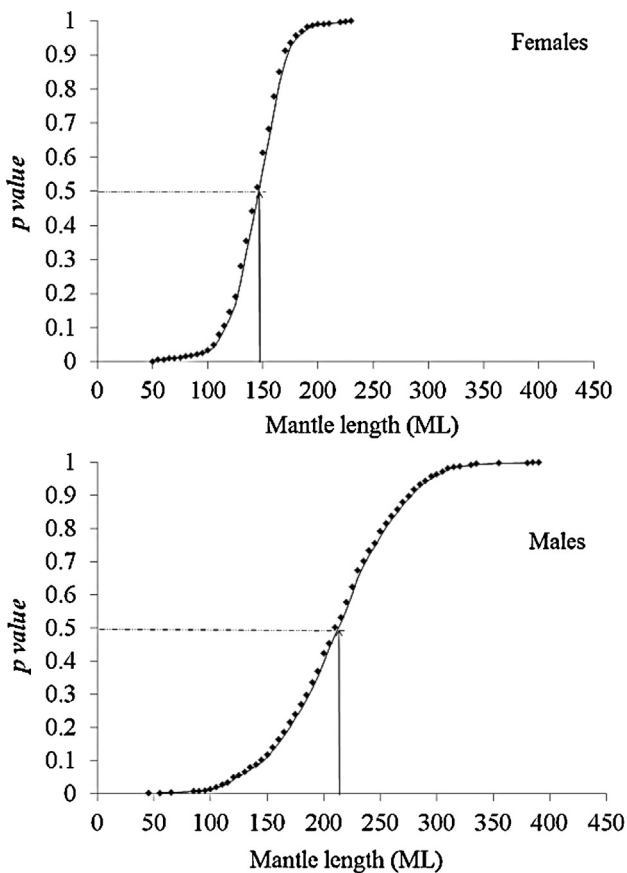


Fig. 4. Cumulative percentage of mature (stages III and IV) female (A) and male (B) of *Doryteuthis plei* per ML category (solid line). ML of 50% of mature squid is indicated.

TL, from 42 mm TL onward, peaking at 51 mm TL (Fig. 6C). In relation to the maturity stages, the same pattern found in females was found in males, where the gonad weight correlated significantly to maturity stage III (Fig. 6D).

In the second model, depth was also found to be a significant factor for males (Table 7). A positive correlation was found between TW and depths from 13 m to 18 m, peaking at 15 m depth (Fig. 6E). No significant relationship was found between TW and fishing areas (Fig. 6F). However, gonad weight peaked in the fishing month March (Fig. 6G). The inter-annual variation was also significant in males, with a positive correlation with TW observed in the 2011–2012 season (Fig. 6H).

4. Discussion

Some characteristics of *D. plei* population structure exploited by the small-scale fisheries of SSI seemed to be very similar to those described from the shelf trawling fishery off the South Brazil Bight (Perez et al., 2002; Rodrigues and Gasalla, 2008), i.e. females being smaller and more robust than the males (which on average were 1.6 times bigger than females), and more abundant during the summer months. This pattern was also observed for other loliginids caught elsewhere, e.g. *L. forbesi* and *L. vulgaris* off the European coast (Pierce et al., 1994; Moreno et al., 1994, 2007; Rocha and Guerra, 1999); *L. reynaudii* in South Africa (Olyott et al., 2006) and *D. pealei* in the North Atlantic Ocean (Dawe et al., 1990). However, in contrast to the shelf fisheries, the hand-jigging around the island catches squid with a larger size as a whole (e.g. maximum ML and higher values of the ML/BW relationship's exponent "b"), which is associated to gear selectivity and to the local occurrence of spawning concentrations. The fact that females were more frequent than males during the

first three months of the fishing season, while males appeared more frequently at the end of the season, confirms the existence of female post-spawning mortality or migration. Regarding the ML/BW relationship, since exponent "b" values were significantly higher in females than in males, and in immature and in-maturation individuals (stages I and II) of both sexes, findings suggest somatic growth during these stages, and reproductive growth in mature and spent squid (stages III and IV).

Our results show that the local small-scale fishery seasonally removes part of the reproductive stock of the squid *D. plei* in shallow waters around the island, as confirmed by the high proportion of mature squid in all samples, with a peak in February. In this sense, all findings refer to the portion of the squid population which is vulnerable to the local hand-jigging fishery, thus, it is not intended to represent the whole population. Also, mated females were present throughout the fishing seasons, as confirmed by the presence of spermatophores in the males' buccal receptacle in all samples.

Previous studies on loliginids reported that size-at-maturity in squid can vary dramatically, depending on the location and time of collection of samples (Raya et al., 1999; Perez et al., 2002; Rodrigues and Gasalla, 2008). The size-at-maturity of squid caught by the shrimp trawling off the coast of São Paulo and Santa Catarina, was relatively smaller than the ones found in SSI by the present study. This may be due to the effect of fishing gear selectivity, as suggested by Martins and Perez (2007) that compared values obtained from squid caught by hand-jigging and fish-traps in Santa Catarina Island.

Postuma and Gasalla (2010) showed that the hand-jigging of *D. plei* squid targets dense concentrations of squid in austral-summer months (November–April), with CPUE peaks between February and March, where sea surface temperature were warmer. Present study confirms that these squid were in reproductive activity, as indicated by the positive correlation between gonad weight and month, for both sexes. According to the hypothesis of Forsythe (2004), warmer temperatures in surface waters during the summer would stimulate somatic and reproductive growth and the development of gonads and gametes in females, which could explain the great lengths and the greater concentration of mature individuals in this coastal region.

In relation to gonadal development, it was found that the ovary enlarges as females grow up to 151–175 mm ML. In females larger than this, the ovary loses weight possibly due to spawning activity. In males, the GAMLSS suggested the co-occurrence of two different groups, one that matures at 187 mm ML and another that matures at 290 mm ML. This kind of pattern among males seems to have been observed in *Loligo vulgaris* caught off southern Portuguese waters (Coelho et al., 1994), *L. vulgaris* and *L. forbesi* males in Galician waters (Guerra and Rocha, 1994) and *D. plei* caught by the industrial trawling off Brazil (Marques and Gasalla, 2002; Perez et al., 2002). Hanlon (1998) and Hanlon et al. (2002) studying the behavior of *Loligo* sp. and *Loligo vulgaris reynaldii* at field in South Africa, used the term "sneakers" for the smaller males and "consorts" for the larger males that formed different reproductive rows during spawning in the seafloor. One could speculate that the small mature males found in present study could correspond to a "sneakers" group and that the group of larger males could correspond to a "consorts" group. Anyway, the fact that the population could have one stratum in males that matures earlier than the other could represent an interesting reproductive strategy for increasing fertilization.

The first GAMLSS model showed a relationship between gonads length and weight in both sexes. In females, the accessory gland weight and nidamental gland length were found to be positively correlated to ovary weight. This was also reported in Sanchez and Demestre (2010), which suggested that nidamental glands could be used as a signal of maturity in females, since the development of the

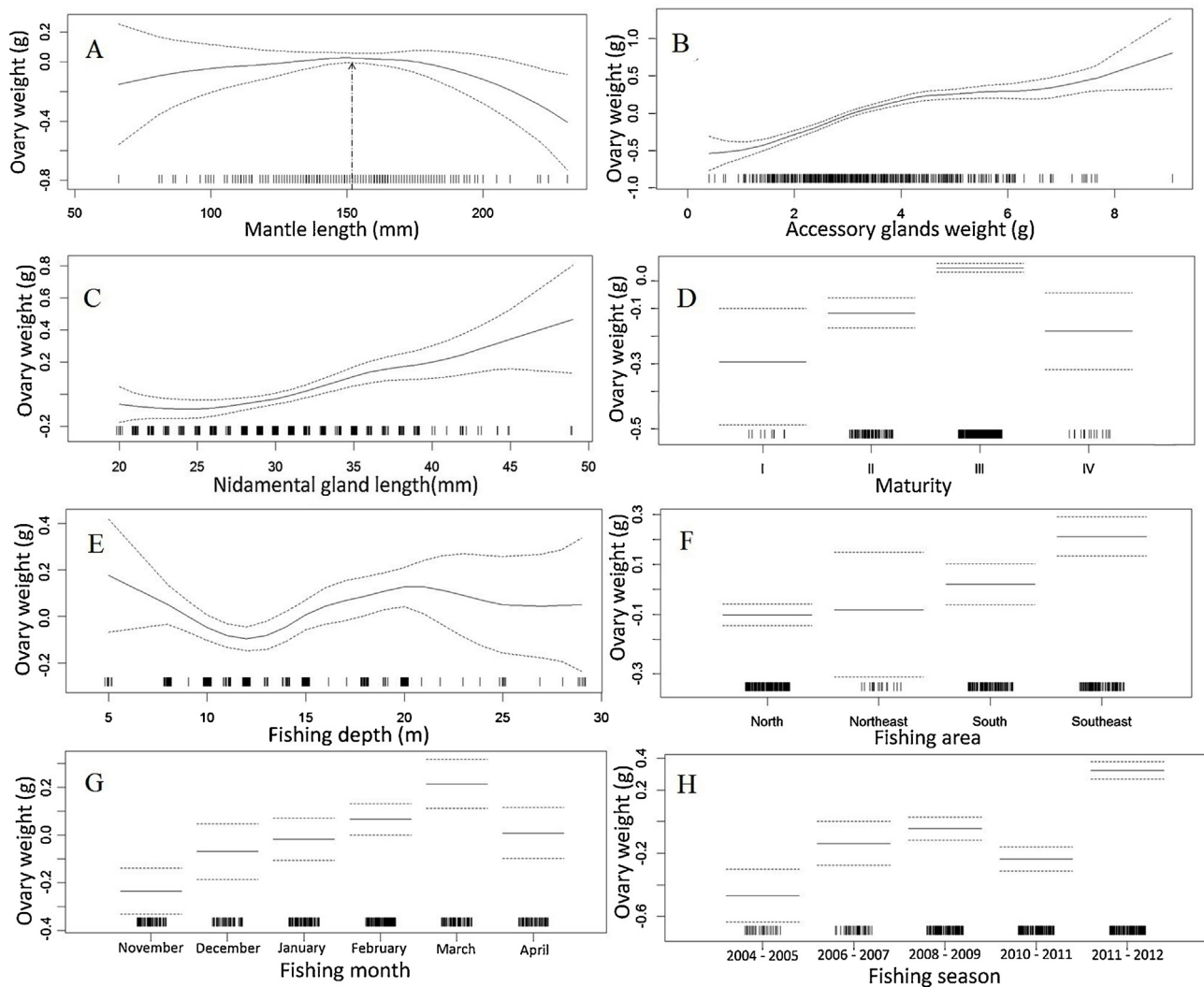


Fig. 5. GAMLSS smoothing curves fitted to partial effects of explanatory variables on reproductive and temporal variables, in females of *Doryteuthis plei*. OW is represented as a function of (A) ML, (B) AGW, (C) NiGL, (D) Mat, (E) Fd, (F) Fa, (G) Fm and (H) Fs. Dashed lines represent 95% confidence intervals around the main effects. The arrow in (A) shows the correlation peaks in relation to the ML.

gland, is well connected to the ovary development, probably linked to the production of gametes. In males, the ML was the variable that better and positively correlated to testis weight. This suggests that the female invest in maximizing egg production to ensure successful spawning, whereas males invest more in somatic growth due the characteristic sexual dimorphism in this genus (i.e. males larger than females), in order to optimize the chances of effective mating with females. However, a peak of testis weight was found when the spermatophoric complex attained 1.3 g of spermatophoric complex, after this the testis loses weight, suggesting the transfer of spermatophores to the females during mating.

Based on the above mentioned model, it may be recommended that for future optimized fishery monitoring initiatives where only length data may be obtained, the NiGL (females) and TL (males) should be the most important biometric variables to monitor the reproductive activity of *D. plei*.

The second GAMLSS model showed that depth (Fd) was the most significant factor influencing the reproductive activity in both sexes, also indicating that it intensifies between 13 m and 23 m, peaking at 15 m depth in males and 20 m in females. The strong correlation found between the gonads weight (OW–TW) and the fishing areas (Fa) indicated a peak occurring in the South and Southeastern areas of the island, coinciding also with the highest mean

GSI, where females were more abundant. However, the lower values of OW in females found in the North and Northeastern areas, from 5 m to 10 m depth, could also indicate an evacuation of the ovary during/after the spawning process. Considering local oceanographic studies, the South and Southeastern areas of the SSI seem to be relatively biologically poorer if compared with the other areas (Pires-Vanin, 2008). Thus, it may be suggested that the sheltered bays of the South and Southeastern areas of SSI could actually be a breeding ground for mating, while the North and Northeast areas may correspond to spawning grounds.

The inter-annual and intra-annual variation of gonadal weight showed a significant peak during February and March and in the 2011–2012 fishing season. The reason why that particular year showed higher values of maturation in comparison to other years should be further investigated by using environmental data series in future studies.

Overall, some further speculation on the aggregation of mature squid in the study area may link the combined effect of the following factors: (i) the wind-driven coastal upwelling events, with intrusion of the SACW stratifying water column in summer (Castro et al., 2008; Martins and Perez, 2007), (ii) changes in environmental variables in the inshore region (Pecl and Jackson, 2008), (iii) the favorable condition of sea surface water temperatures (Postuma

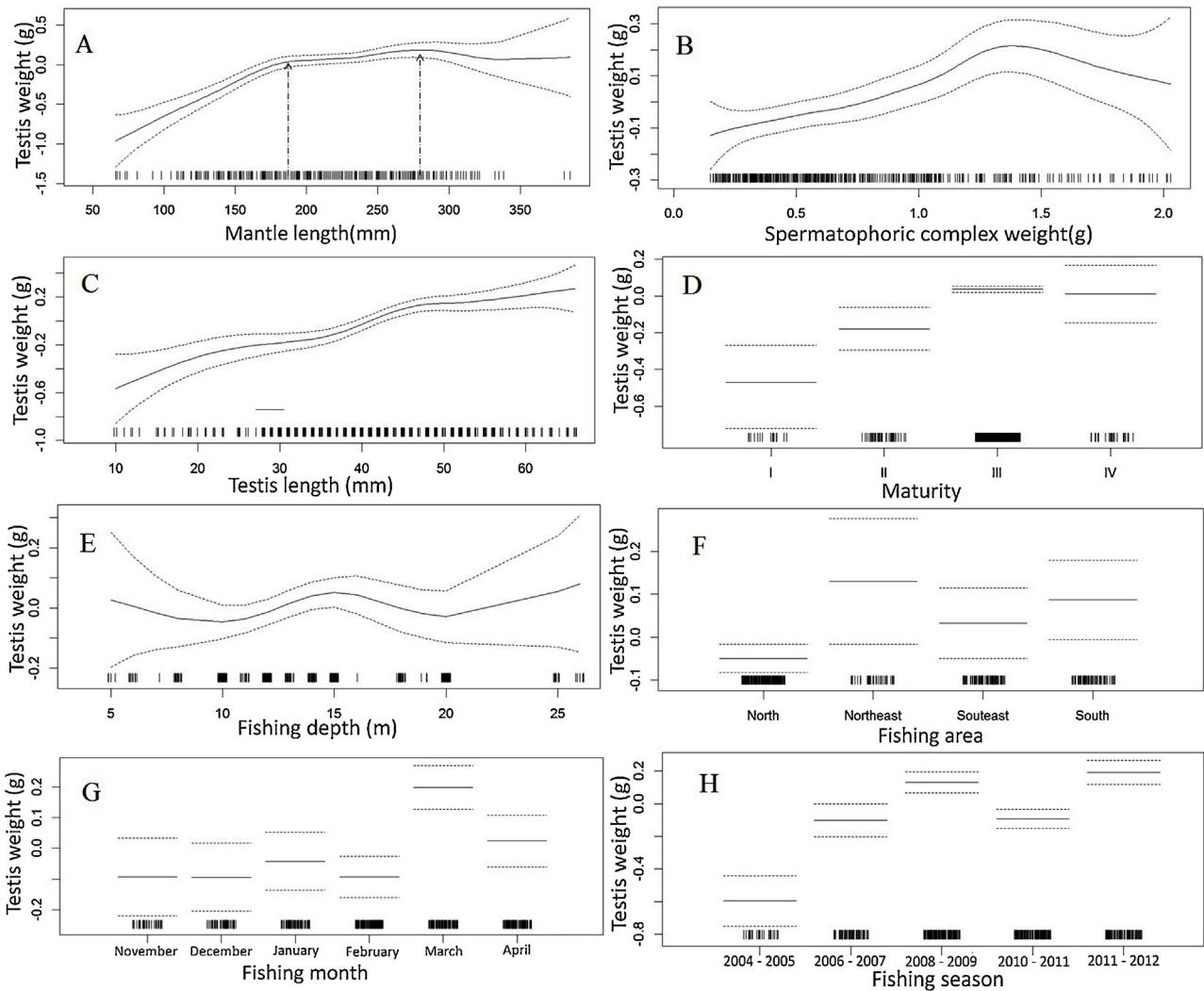


Fig. 6. GAMLSS smoothing curves fitted to partial effects of explanatory variables on reproductive and temporal variables, in males of *Doryteuthis plei*. TW is represented as a function of (A) ML, (B) SW, (C) TW, (D) Mat, (E) Fd, (F) Fa, (G) Fm and (H) Fs. Dashed lines represent 95% confidence intervals around the main effects. The arrow in (A) shows the correlation peaks in relation to the ML.

and Gasalla, 2010), (iv) food availability (Gasalla et al., 2010), and (v) reproductive strategies (Rocha et al., 2001) somehow favored by island's environment.

Finally, the spatial-temporal pattern of reproductive activity found here may be useful in drafting specific studies to detect spawning grounds of *D. plei* in the region, as well as in the definition of future fisheries management plans.

5. Conclusions and summary

The SSI was evidenced as an important reproductive area for *D. plei* in the South Brazil Bight area. The combination of spatial-temporal factors (depth, area, month, and year) helped understanding the pattern of squid aggregation for reproductive activity around the island, while non-linear correlations between reproductive structures were useful to identify the biometric variables that better described maturation. The GAMLSS showed advantages to identify long-term reproductive patterns, which would be unlikely possible by using the gonado-somatic index alone.

In summary, the following spawning scenario was proposed for the species in the region, with a peak of reproductive activity during February and March. The concentration of mature organisms

predominated in the Southern and Southeastern coasts of SSI, where the largest sheltered bays are located. It suggests that favorable breeding grounds for mating may be located in these areas, while the North and Northeast ones seem to represent spawning grounds. Females were more frequent at the beginning of the fishing season (November and December), concentrating in shallow waters to spawn. During the reproductive activity peak in February, the sex ratio tended to equalize (1:1) at depths of 10–20 m, where squid would most likely be mating. Local fishers seem to track this trend of aggregation.

Lastly, present findings should assist the future development of management measures (e.g. for seasonal, size, and spawning area protection) aiming the sustainable use of the resource.

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