

REGULAR PAPER

Condition analysis of the Brazilian sharpnose shark *Rhizoprionodon lalandii*: evidence of maternal investment for initial post-natal life

Jessica T. Corso¹  | Otto B. F. Gadig²  | Rodrigo R. P. Barreto³  | Fabio S. Motta¹ 

¹Laboratório de Ecologia e Conservação Marinha (LABECMAR), Instituto do Mar, Universidade Federal de São Paulo (UNIFESP), Santos, Brazil

²Laboratório de Pesquisa de Elasmobrânquios, Instituto de Biociências, Universidade, Estadual Paulista – UNESP, Campus do Litoral Paulista, São Vicente, Brazil

³Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul do Brasil (CEPSUL/ICMBio), Itajaí, Brazil

Correspondence

Fabio S. Motta, Laboratório de Ecologia e Conservação Marinha (LABECMAR), Instituto do Mar, Universidade Federal de São Paulo (UNIFESP), Rua Dr. Carvalho de Mendonça, 144, Santos SP 11070-100, Brazil.
Email: limbatus@gmail.com

The present study analysed the condition factor (K) and the hepato-somatic index (I_H) of the Brazilian sharpnose shark *Rhizoprionodon lalandii* during its entire life cycle. Discontinuity of liver growth was observed after sexual maturity. High condition values were recorded in the length classes of 300–350 mm (neonates), when the livers represented about 8% of total mass, decreasing until the length classes of 400–450 and 450–500 mm in females and males, respectively. Seasonal analysis exhibited low I_H values in the summer, while for K , low values were in spring, indicating greater investment for body growth during spring and for gonad maturation in summer. Such findings indicate that this small coastal shark species accumulates reserve substances in the liver that will be used during reproduction. The decline in I_H values in juveniles suggests that reserves provisioned by the mother to the neonate liver can be used in the first months of life.

KEYWORDS

condition factor, elasmobranch, hepato-somatic index, maternal investment, reproduction

1 | INTRODUCTION

Analysing the degree of well-being (condition) of an animal is strategic in evaluating vital processes such as migration, feeding and reproduction. Condition reflects the accumulation of energy for future use to alleviate the effects of scarcity of food resources and the costs of reproductive and migratory activities (Gallagher *et al.*, 2014; Irschick & Hammerschlag, 2014). Despite its importance, studies about the condition of elasmobranchs are scarce compared with teleosts, mostly due to the relative smaller participation of sharks and rays in total fishery production, lack of systematic monitoring of fisheries landings, difficulty in accessing whole specimens and the migratory habits of many species (Castro *et al.*, 1999; Hussey *et al.*, 2009).

Fish condition indicators are traditionally calculated based on the length–mass relationship (Bolger & Connolly, 1989; Froese, 2006; Jakob *et al.*, 1996) as the condition factor and metrics that relate mass of organs with total mass (Hussey *et al.*, 2009), such as liver (hepato-somatic index) and gonads (gonado-somatic index). Recently, biochemical analysis (e.g. fatty acids) and the relationship between circumference and body length measures have also been used for large sharks (Gallagher *et al.*, 2014; Irschick & Hammerschlag, 2014). In elasmobranchs, condition metric fluctuations have usually been related

with energetic costs during the reproductive cycle (Allen & Cliff, 2000; Capapé & Reynaud, 2011; Estalles *et al.*, 2008; Fermin & Bashirulah 1984; Grijalba-Bendeck *et al.*, 2008; Hoffmayer *et al.*, 2006; Machado *et al.*, 2001; Peres & Vooren, 1991), migration (King, 1984), responses to variations in food availability (Oddone & Amorim, 2007) and other factors that influence the well-being of organisms (Braccini & Chiaramonte, 2002; Hoffmayer *et al.*, 2006; Parsons & Hoffmayer, 2005).

Placental viviparity is usually regarded as the most efficient reproductive strategy among elasmobranchs due to the close relationship of nutrient demand and support between the embryos and the mother (Parsons *et al.*, 2007). According to Hussey *et al.* (2010), maternal investment extends to postnatal life of two shark species with biennial reproductive cycles, the dusky shark *Carcharhinus obscurus* (LeSueur 1818) and spinner shark *Carcharhinus brevipinna* (Valenciennes 1839), which have enlarged livers in the new-born. This condition would assist with the beginning of foraging activities and increase survival probability during the first weeks and months of life.

The sharpnose sharks, genus *Rhizoprionodon* Whitley 1929 are represented worldwide by at least seven small coastal placental species (up to 1,780 mm total length; L_T) with annual reproductive cycles and concurrent ovarian and gestation cycles (Compagno, 1984). The

Brazilian sharpnose shark *Rhizoprionodon lalandii* (Valenciennes 1839) is the most abundant coastal shark species in south-eastern Brazil, comprising approximately 60% of total shark landings in artisanal fisheries (Motta *et al.*, 2005). In the same area, the species attains a maximum size of 800 mm L_T and sexual maturity at 590–650 mm L_T (Motta *et al.* 2007). Moreover, three seasonal occurrence patterns related to size classes are recognized: August–September neonates are most frequent; November–March, juveniles are most common; April–July, adults are the most numerically abundant (Motta *et al.* 2007). Data on condition of *R. lalandii* are minimal and available in few biological studies with broader scope. For instance, in northern Brazil, Lessa (1988) recorded the liver energetic reserves for females at the end of gestation, while Andrade *et al.* (2008) associated temporal variations of the condition factor with the reproductive period of the species on the southern coast.

In this context, the present work reports an analysis of condition of *R. lalandii* from a long-term data set from the sharks caught by the artisanal fishery in south-eastern Brazil. The aim of the present study was to assess two condition metrics (condition factor and hepatosomatic index) by length classes and seasons as models for small coastal placental sharks with annual reproductive cycles.

2 | MATERIALS AND METHODS

2.1 | Sampling

Specimens of *R. lalandii* ($n = 8,268$) were obtained weekly from artisanal fisheries operating along the south-central coast of São Paulo State, south-eastern Brazil and landed at Pescadores Beach, Itanhaém municipality ($24^\circ 11' S$; $46^\circ 48' W$; Figure 1), between January 1997 and December 2003. The fishing fleet consisted of small motorized boats (4–10 m long) using 1,500 m long monofilament gillnets with stretched-mesh sizes of 7, 12 and 14 cm. The nets were set c. 5–20 km from the shore in waters between 5 and 35 m deep. All landed sharks were sexed, measured (L_T , mm) and weighed (total body mass, M_T , g). After evisceration by fishermen still on the beach for commercial purposes, the livers were weighed in g ($n = 2,071$).

2.2 | Relative growth of liver and condition metrics

The relative growth of the liver and hepatosomatic index (I_H) were studied for 893 females and 1,178 males. Relative growth of the liver was analysed using the allometric equation $M_H = a L_T^b$, where M_H is the total liver mass, L_T total length and a and b are parameters estimated by least-squares fitting method after log-transformation of M_H and L_T data. The hepatosomatic index (I_H) was calculated by the expression $I_H = 100M_HM_T^{-1}$, where M_H is the total liver mass and M_T is the total body mass.

Fulton's condition Factor (K) was calculated for 3,962 females and 4,306 males by the expression $K = M_T(L_T^b)^{-1}$ (Fulton, 1904), where M_T is the total body mass, L_T total length and b is the regression coefficient of the length–mass relationship $M_T = a L_T^b$. In the present study values for b of 3.22 and 3.13 were used for females and males, respectively (Motta *et al.*, 2014). Linear regressions of M_H and L_T were

calculated separately for females and males and then compared by analysis of co-variance (ANCOVA).

Time-series of K and I_H , by quarter of the year and length classes (50 mm) were generated for females and males using generalized linear models (GLM). Like other predictive models, GLMs allow removal of unsystematic variations caused by some components (*i.e.* variables) and identify systematic trends or signals in the data. The basic GLM structure used in this study was: $\mu = X\beta$, where X is the matrix of explanatory variables, β is the vector of explanatory variables and μ is the expected values for response variables.

The GLMs fitted to both response variables (K and I_H) in both time-series scenarios (quarter and quarter of the year) used year, quarter of the year, season and length class (50 mm range) as independent class variables and the L_T as an independent continuous variable. Exclusively for I_H , we considered in the modelling process the inclusion of K as a continuous independent variable. We chose not to use I_H while modelling K , to avoid a significant reduction in the number of observations of this variable (significantly higher than I_H in this study: 8268 v. 2071). Models were then refined by interactively selecting the most appropriated combination of explanatory variables according to their statistical significance.

3 | RESULTS

3.1 | Relative liver growth

The analysis of the relationship between M_H and L_T (Figure 2) showed a tendency for continuous growth until the sizes at first maturity, after which a great dispersion of data was observed. The co-variance analysis revealed significant differences between M_H and L_T relationships of females and males for *R. lalandii* (between the regression coefficients $F_{1,2070} = 4,154$, $P < 0.001$, between the intercepts $F_{1,2070} = 4,054$, $P < 0.001$).

3.2 | Condition metrics analysis

Significant differences between the length classes for I_H (Figure 3 and Tables S1 and S2) and K (Figure 4 and Tables S3 and S4) were detected. Both metrics showed high values for length classes of neonates (300–350 mm L_T), decreasing to the classes between 400 and 500 mm L_T . From these length classes, a gradual increase of I_H and K were observed, especially for the females (Figures 3 and 4).

The variables selected to build the model structure that best explains each variable response of this study (K and I_H), as well as the estimated coefficients and their respective indices of statistical significance are available in the Supporting Information (Tables S1–S5). In general, the best model for both K and I_H comprised only quarter of the year and length class (Tables S1–S4). However, considering that in the analysis of I_H the variable K was also tested through GLM analysis, we found the same significance during the modelling process as shown in Tables S1 and S2.

Due to high co-linearity, our models did not converge when seasons (summer, autumn, winter and spring) and quarter of the year (1997 summer, 1997 autumn *et seq.*) were placed together. Hence, we additionally performed a sensitivity analysis of K and I_H in relation to



FIGURE 1 The fishing area and landing beach of the artisanal fishery fleet in Itanhaém municipality, São Paulo State, southern Brazil where samples of *Rhizoprionodon lalandii* were gathered

season only (Figure 5 and Table S5). In these additional analyses, there were significant seasonal differences for I_H (Figure 5 and Table S5). Low I_H values were observed during the summer for both sexes. In other seasons, high equivalent values were recorded in the winter–spring period for females while the highest value for males was observed in the autumn. Regarding K , (Figure 5 and Table S5), low values for both sexes were found in the spring while high equivalent values were observed in the other seasons, except in the summer for females.

According to GLM-derived time series of seasonal mean values of K , the spring presented the lowest value in four of the 7 years: 1998, 1999, 2001 and 2003, in both sexes (Figure 6). The significant differences detected between analysed factors indicated high interannual variability in the condition of the species (Tables S3 and S4). The GLM-derived time series of seasonal mean values of I_H (Figure 7) did not present a clear trend, possibly due to low sample size, mainly from the year 2001. Nevertheless, significant differences were also detected (Tables S1 and S2) in a small fraction of the analysed factors when compared with K analyses.

4 | DISCUSSION

Given the difficulties in obtaining data on commercially caught sharks, the present study represents one of the largest and most comprehensive (8,268 individuals) on the condition metrics of a shark species. The discontinuities demonstrated in development of the liver after attaining sexual maturity may be explained by the presence of individuals at different stages of the reproductive cycle in the sample, indicating the participation of the liver in the reproduction of the species. The performance of liver reserves in energy-consuming activities, such as reproduction, has already been documented for other elasmobranchs (Hoffmayer *et al.*, 2006; Hussey *et al.*, 2009; Lteif *et al.*, 2016; Peres & Vooren, 1991; Pethybridge *et al.*, 2014). Some authors have emphasized the importance of the reserves for vitellogenesis and gestation of females (Gallagher *et al.*, 2014; Peres & Vooren, 1991; Rochowski *et al.*, 2015), including *R. lalandii* in northern Brazil, where Lessa (1988) recorded a doubling of liver mass in females at the end of gestation. In the present study, discontinuity of liver growth after

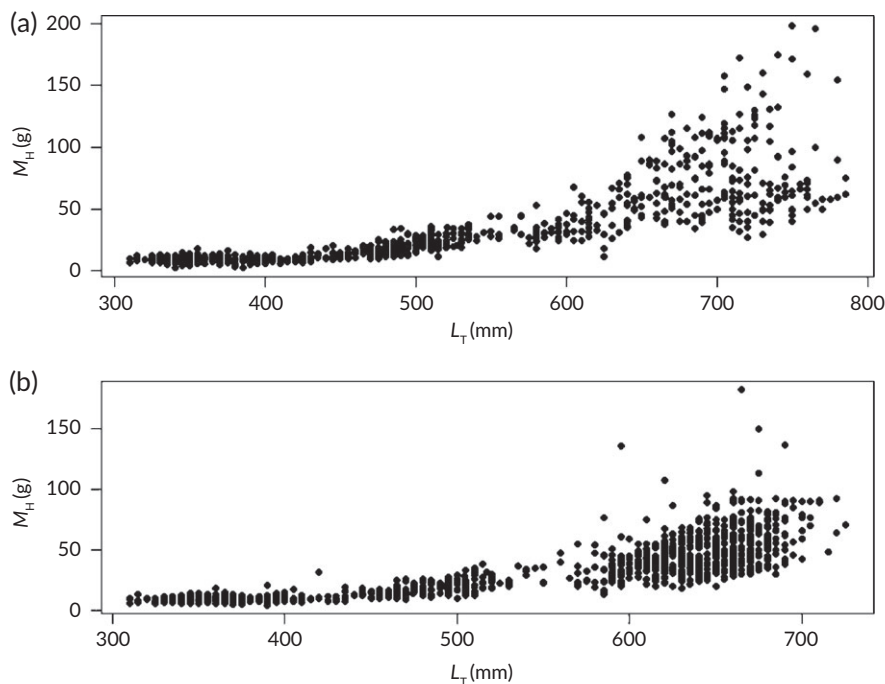


FIGURE 2 Relationship between liver mass (M_H) and total length (L_T) of (a) female ($y = 0.0000002x^{3.0}$, $R^2 = 0.85$, $P < 0.001$, $n = 893$) and (b) male ($y = 0.0000003x^{2.89}$, $R^2 = 0.85$, $P < 0.001$, $n = 1,178$) *Rhizoprionodon lalandii*

sexual maturity was observed, with both sexes showing significant differences, although they were more prominent for females.

The high condition observed for neonates, detected in both K and I_H , was associated with the possible transfer of energy reserves from the mother to the offspring; here, the I_H reaches 6–8% for females and males, respectively. Evidence of maternal investment for postnatal life has also been reported for two viviparous shark species with biennial

reproductive cycles, *C. obscurus* and *C. brevipinna* (Hussey *et al.*, 2010). According to these authors, this strategy maximizes the chances of survival in the first few months of life, during the development of foraging skills of the individuals. In *R. lalandii*, the investment is relevant because of the small birth size and the shared use of the same nursery area with at least four larger shark species (Gadig *et al.*, 2002; Motta *et al.*, 2005). The liver reserve depleted in 400–500 mm length classes of juveniles,

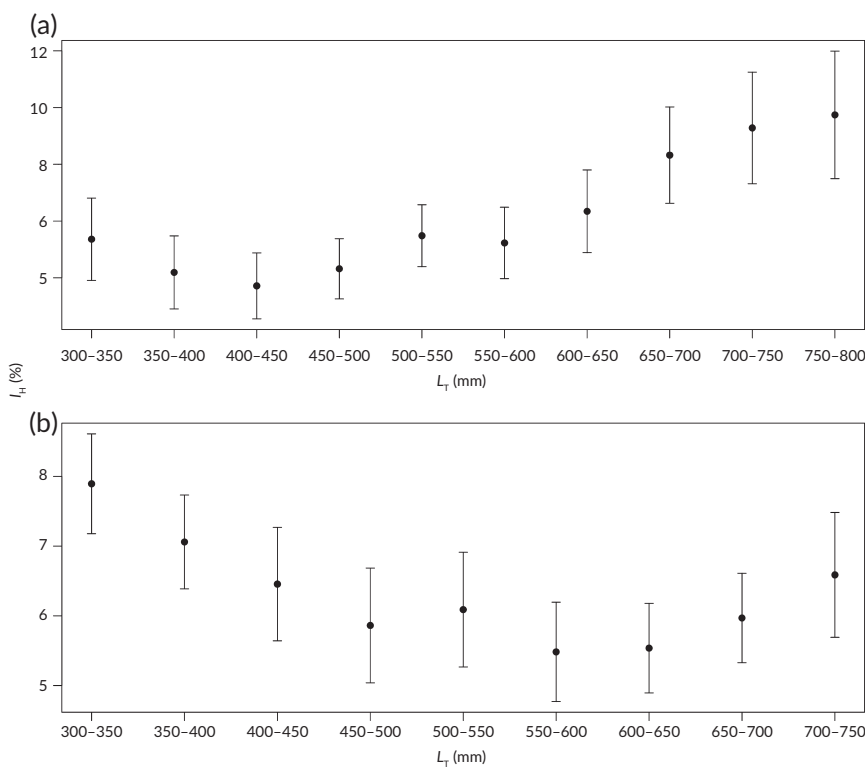


FIGURE 3 Trends in generalized linear model standardized mean ($\pm 95\%$ C.I.) hepato-somatic indices (I_H) for total-length (L_T) classes of (a) female and (b) male *Rhizoprionodon lalandii*

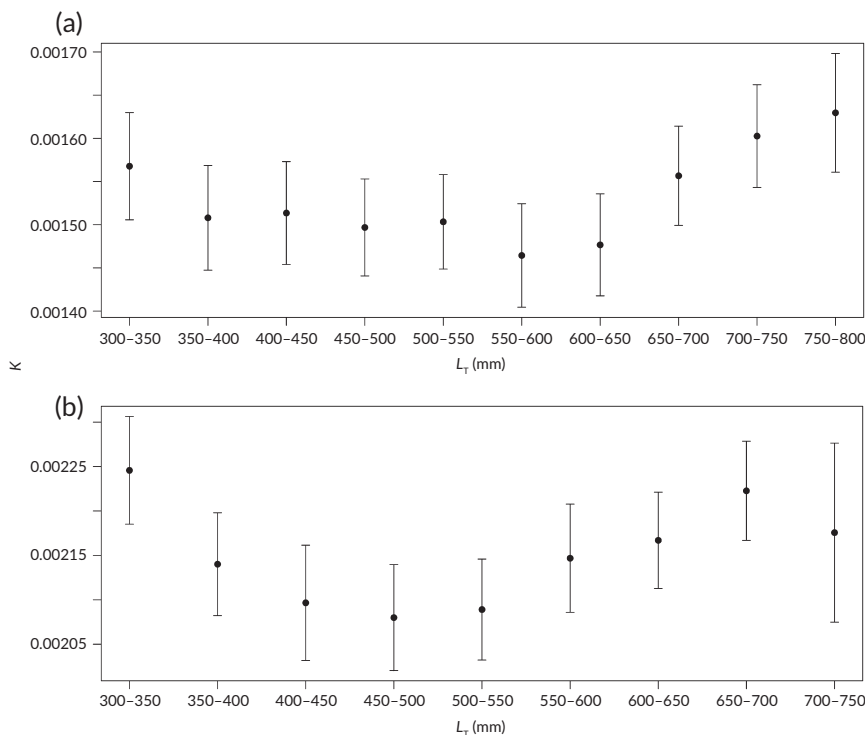


FIGURE 4 Trends in generalized linear model standardized mean ($\pm 95\%$ C.I.) Fulton's condition factor (K) for total-length (L_T) classes of (a) female and (b) male *Rhizoprionodon lalandii*

where the I_H had the lowest value in the life cycle (c. 4% for females and 6% for males). Coincidentally, vertebrae sectioned from specimens of these size classes show additional band pairs after the birthmark, which may indicate physiological stress at this life stage (F. S. Motta, pers. comm.). In Hawaii, natural mortality of juvenile scalloped hammerhead shark *Sphyrna lewini* (Griffith & Smith 1834) was associated with poor condition during the first months of life (Duncan & Holland, 2006). The hypothesis of maternal investment for postnatal life may have been little studied due to the difficulty of access to neonates in previous condition investigations. Most studies do not cover this age group (Andrade *et al.*, 2008; Hoffmayer *et al.*, 2006; Peres & Vooren, 1991), either because sampling did not occur in nursery areas or because of the selectivity of the fishing gear.

Motta *et al.* (2007) showed that juvenile *R. lalandii* predominate between November and March, with the transition between neonates and juveniles occurring in October. Thus, the low value of K during spring may be evidence of the directing of energy obtained from feeding for corporal growth of young individuals that do not yet invest in reproduction. During summer, K values are high once more, although I_H shows the lowest value in this season, possibly reflecting an investment in gonad maturation from the accumulated energy in the liver. According to Motta *et al.* (2007), mating in the study area takes place between April and June for first-maturing females and between July and September for post partum females (southern hemisphere autumn and winter respectively), where both condition metrics show high values, indicating the level of energetic demand required for this critical phase of the life cycle. A similar pattern was recorded for the milk shark *Rhizoprionodon acutus* (Rüppell 1837) off the Senegal coast (Ba *et al.*, 2013). On the other hand, Machado *et al.* (2001) associated the highest I_H values of the Caribbean sharpnose shark *Rhizoprionodon*

porosus (Poey 1861) in north-east Brazil with the period before reproduction, which is the opposite of that observed in the present study.

Regarding K analyses for the 7 years sampled, the great magnitude of variation is highlighted in 1998, with one of the highest and the lowest values within the whole set of samples, in autumn and spring respectively. The 1997–1998 the El Niño phenomenon was one of the strongest events ever recorded in Peruvian waters (García & Vieira, 2001), with worldwide effects. In south-eastern Brazil, low salinity in estuaries, increased rainfall and increased water surface temperature occurred between July 1997 and September 1998 (García & Vieira, 2001). In this same region, significant changes in species composition and patterns of diversity were found in the years of intense El Niño (1983–1984 and 1997–1998), with marine fish visiting estuaries less often (García & Vieira, 2001; Paes & Moraes, 2007).

The influence of climatic phenomena on reproduction and feeding, prolonging the spawning period and causing weight loss, has already been observed for teleost species (Dioses *et al.*, 2002; Martínez *et al.* 1985; Santander & Zuzunaga, 1984), but studies of effects on elasmobranchs are still limited. One study on the effect of El Niño on the condition of Peruvian hake *Merluccius gayi peruanus* (Guichenot 1848) showed that during the phenomenon condition values were low, mainly for the year 1998 (Ballón *et al.*, 2008). Otherwise, in Greenland, the condition of the Atlantic cod *Gadus morhua* L. 1,758 was positively related to the increase in water temperature (Lloret & Rätz, 2000). For the Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson 1836), although not during an El Niño, decrease of condition related to increase of water temperature and consequent increase in oxygen consumption (Hoffmayer *et al.*, 2006; Parsons & Hoffmayer, 2005) was recorded. The authors suggested that the sharks should increase their feeding intensity or mobilize energy reserves to supplement the low

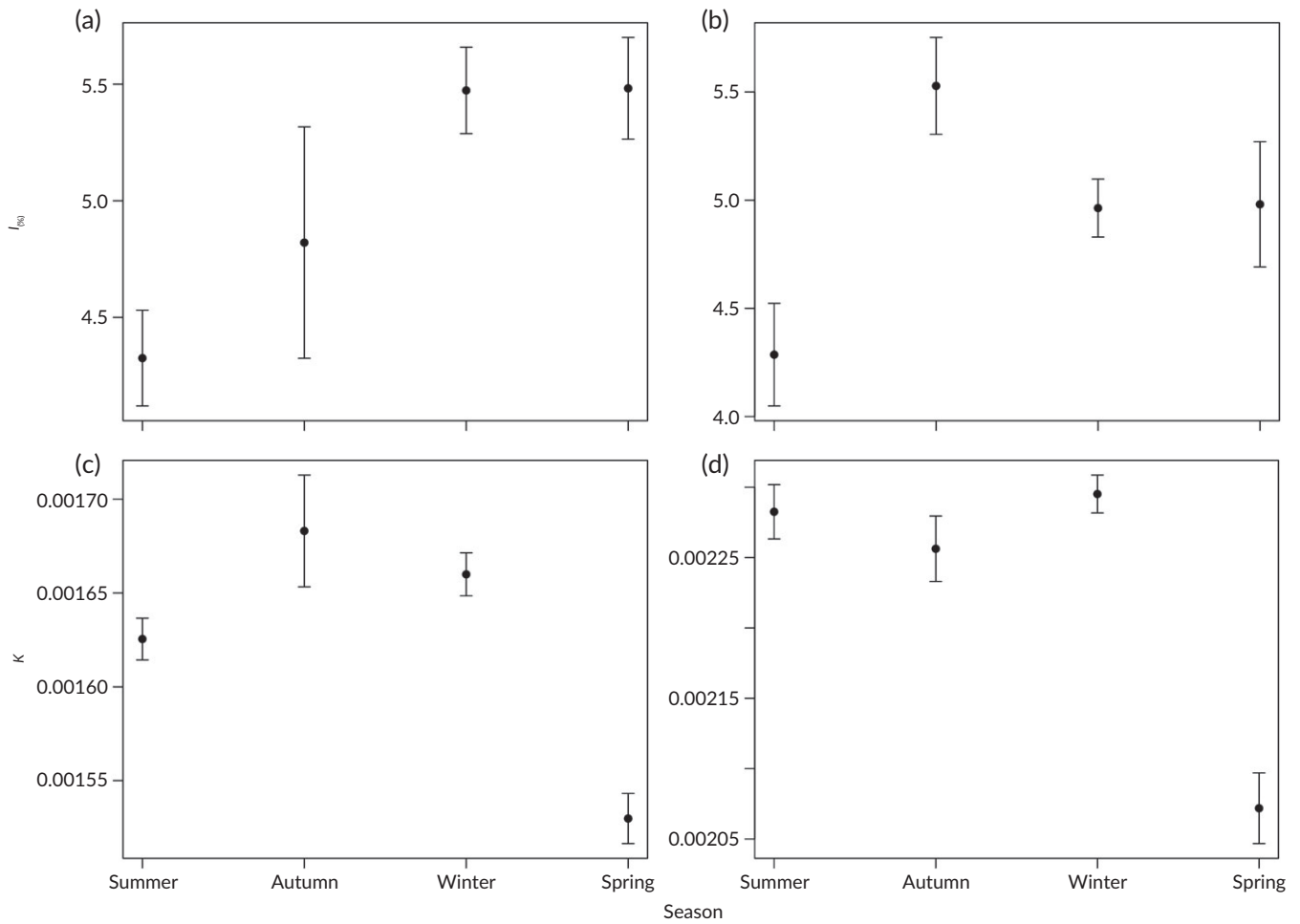


FIGURE 5 Trends in generalized linear model standardized mean ($\pm 95\%$ C.I.) (a), (b) hepato-somatic index (I_H) and (c), (d) Fulton's condition factor (K) by seasons for (a), (c) female and (b), (d) male of *Rhizoprionodon landii*

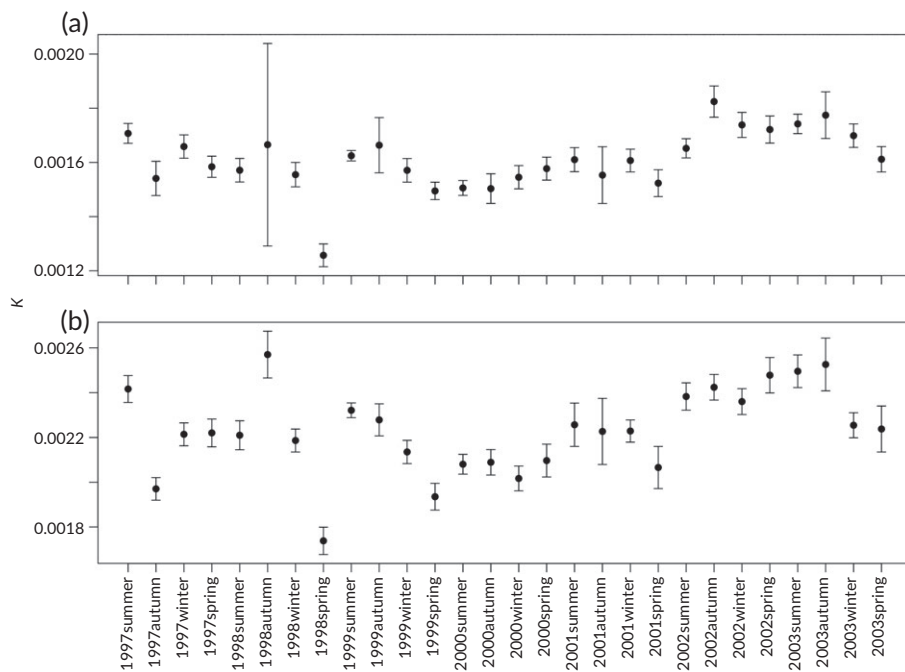


FIGURE 6 Trends in generalized linear model standardized mean ($\pm 95\%$ C.I.) Fulton's condition factor (K) between January 1997 and December 2003 for (a) female and (b) male *Rhizoprionodon landii*

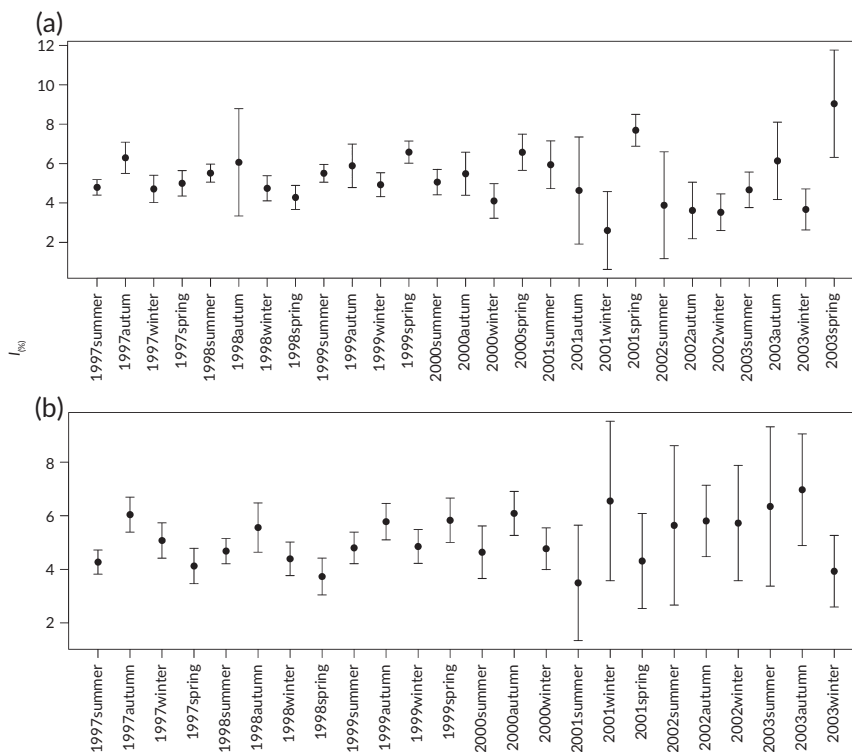


FIGURE 7 Trends in generalized linear model standardized mean ($\pm 95\%$ C.I.) hepato-somatic index (I_H) between January 1997 and December 2003 for (a) female and (b) male *Rhizoprionodon landii*

condition. In the present study, summer, autumn and winter seasons of 1998 correspond to a period of increasing water temperature (Garcia & Vieira, 2001) and *R. landii* exhibit high condition values, which may indicate that the species was able to maintain its well-being even under such circumstances. On the other hand, after the El Niño effects in the spring of 1998, its condition decreased drastically. In fact, more detailed studies are necessary to establish the relationship between the El Niño phenomenon and elasmobranch condition.

It was possible to describe seasonal variations in the condition of *R. landii*, despite the annual reproductive cycle with concurrent vitellogenesis and gestation. In some periods the interpretation of the results was difficult because of the occurrence of specimens at different life-cycle stages. The study also highlights the relevance of the liver in reproduction, accumulating energy for the beginning of post-natal life in neonates and for gonad maturation in adults.

ACKNOWLEDGEMENTS

The authors thank the fishermen of Itanhaém for their collaboration with PROJETO CAÇÃO, for their friendship and permission to examine all sharks landed and to the Brazilian Council for Scientific Research (CNPq) by the grants to J. T. Corssó, and to São Paulo Research Foundation (FAPESP grant # 1999/04085-1) by the grants to F. S. Motta and to the Brazilian Council for Scientific Research (CNPq) by the grants to O. B. F. Gadig.

AUTHOR CONTRIBUTIONS

J.T.C. contributed with ideas, data analysis and manuscript preparation; O.B.F.G. contributed with data collection and manuscript

preparation; R.R.P.B. contributed with the data analysis improvement using generalized linear model (GLM) and manuscript revision; F.S.M. contributed with delineating, data collection and data analysis and manuscript preparation.

ORCID

Jessica T. Corssó [ID https://orcid.org/0000-0001-7643-8795](https://orcid.org/0000-0001-7643-8795)

Otto B. F. Gadig [ID https://orcid.org/0000-0002-8109-5085](https://orcid.org/0000-0002-8109-5085)

Rodrigo R. P. Barreto [ID https://orcid.org/0000-0002-5737-9416](https://orcid.org/0000-0002-5737-9416)

Fabio S. Motta [ID https://orcid.org/0000-0002-8009-8890](https://orcid.org/0000-0002-8009-8890)

REFERENCES

- Allen, B. R., & Cliff, G. (2000). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 9. The spinner shark *Carcharhinus brevipinna* (Müller and Henle). *South African Journal of Marine Science*, 22, 199–215.
- Andrade, A. C., Silva-Junior, L. C., & Vianna, M. (2008). Reproductive biology and population variables of the Brazilian sharpnose shark *Rhizoprionodon landii* (Müller & Henle 1839) captured in coastal waters of South-Eastern Brazil. *Journal of Fish Biology*, 72, 473–484.
- Ba, A., Ba, C. T., Diouf, K., Ndiaye, P. I., & Panfili, J. (2013). Reproductive biology of the milk shark *Rhizoprionodon acutus* (Carcharhinidae) off the coast of Senegal. *African Journal of Marine Science*, 35(2), 223–232.
- Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., & Bertrand, A. (2008). The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayiperuanus*. *Progress in Oceanography*, 79, 300–307.
- Bolger, T., & Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. *Journal Fish Biology*, 34, 171–182.
- Braccini, J. M., & Chiaramonte, G. E. (2002). Reproductive biology of *Psammobatis extenta*. *Journal of Fish Biology*, 61, 272–288.
- Capapé, C., & Reynaud, C. (2011). Maturity, reproductive cycle and fecundity of the spiny dogfish *Squalus acanthias* (Chondrichthyes: Squalidae)

- off the Languedocian coast (southern France, northern Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, 91(8), 1627–1635.
- Castro, J. I.; Woodley, C. M.; Brudek, R. R. (1999). *A preliminary evaluation of the status of shark species* (FAO Fisheries Technical Paper 380). Retrieved from www.fao.org/docrep/003/X2352E/X2352E00.HTM
- Compagno, L. J. V. (1984) FAO Species Catalogue vol. 4, Sharks of the world. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 2. Carcharhiniformes. FAO Fisheries Synopsis 4(125). Retrieved from www.fao.org/docrep/009/ad123e/ad123e00.HTM
- Dioses, T., Dávalos, R., & Zuzunaga, J. (2002). El Niño 1982-1983 and 1997-1998: Effects on Peruvian jack mackerel and Peruvian chub mackerel. *Investigaciones Marinas*, 30(1), 185–187.
- Duncan, K. M., & Holland, K. N. (2006). Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series*, 312, 211–221.
- Estalles, M., Perez Comesana, J. E., Tamini, L. L., & Chiaramonte, G. E. (2008). Reproductive biology of the skate, *Rioraja agassizii* (Müller and Henle, 1841), off Puerto Quequén, Argentina. *Journal of Applied Ichthyology*, 25(1), 60–65.
- Fermin, E. G., & Bashirulah, A. K. M. (1984). Relacion longitud-peso y hábitos alimenticios de *Rhizoprionodon porosus* Poey 1861 (Fam. Carcharhinidae) en el oriente de Venezuela. *Boletín Del Instituto Oceanográfico de Venezuela. Oriente*, 23, 49–54.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: History, meta-analysis and recommendation. *Journal of Applied Ichthyology*, 22, 241–253.
- Fulton, T. W. (1904). The rate of growth of fishes. *22nd Annual Report of the Fisheries Board of Scotland* 1903, 141–241.
- Gadig, O. B. F.; Motta, F. S. & Namora, R. C. (2002). Projeto Cação – a study on small coastal sharks in São Paulo, southeast Brazil. *Proceedings of the International Conference on Sustainable Management of Coastal Ecosystems* (Duarte, P., ed.), pp. 239–246. Porto, Portugal: Fernando Pessoa University. Retrieved from www.researchgate.net/publication/268512689_Projeto_Cacao_-_A_study_on_small_coastal_sharks_in_Sao_Paulo_southeast_Brazil
- Gallagher, A. J., Wagner, D. N., Irschick, D. J., & Hammerschlag, N. (2014). Body condition predicts energy stores in apex predatory sharks. *Conservation Physiology*, 2(1), 1–8.
- García, A. M., & Vieira, J. P. (2001). O aumento da diversidade de peixes no estuário da Lagoa dos Patos durante o período de El Niño 1997-1998. *Atlantica*, 23, 85–96.
- Grijalba-Bendeck, M.; Acero P., A. & González, E. (2008). Biología reproductiva de *Rhinobatos percellens* (Walbaum, 1792) (Batoidea: Rajiformes) en el Caribe colombiano. *Revista de Biología Marina y Oceanografía* 43(3): 469–481.
- Hoffmayer, E. R., Parsons, G. R., & Horton, J. (2006). Seasonal and inter-annual variation in the energetic condition of adult male Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the northern Gulf of Mexico. *Journal of Fish Biology*, 68, 645–653.
- Hussey, N. E., Cocks, D. T., Dudley, S. F. J., McCarthy, I. D., & Wintner, S. P. (2009). The condition conundrum: Application of multiple condition indices to the dusky shark *Carcharhinus obscurus*. *Marine Ecology Progress Series*, 380, 199–212.
- Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., & MacNeil, M. A. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology*, 79, 184–193.
- Irschick, D. J., & Hammerschlag, N. (2014). A new metric for measuring condition in large predatory sharks. *Journal of Fish Biology*, 85(3), 917–926.
- Jakob, E. M., Marshall, S. D., & Uetz, G. W. (1996). Estimating fitness: A comparison of body condition indices. *Oikos*, 77, 61–67.
- King, K. J. (1984). Changes in condition of mature female rig (*Mustelus lentidulatus*) from Golden Bay in relation to seasonal inshore migrations. *New Zealand Journal of Marine and Freshwater Research*, 18(1), 21–27.
- Lessa, R. P. T. (1988). Premières observations sur la biologie reproductive de *Rhizoprionodon lalandei* (Valenciennes, 1839) (Pisces Carcharhinidae) de la côte nord du Brésil – Maranhão. *Revista Brasileira de Biologia*, 48(4), 721–730.
- Lloret, J., & Rätz, H. J. (2000). Condition of cod (*Gadus morhua*) off Greenland during 1982-1998. *Fisheries Research*, 48, 79–86.
- Lteif, M., Mouawad, R., Khalaf, G., Lenfant, P., & Verdoit-Jarraya, M. (2016). Population biology of an endangered species: The common guitarfish *Rhinobatos rhinobatos* in Lebanese marine waters of the eastern Mediterranean Sea. *Journal of Fish Biology*, 88, 1441–1459.
- Machado, M. R. B., Almeida, Z. S., & Castro, A. C. L. (2001). *Estudo da biologia reproductiva de Rhizoprionodon porosus Poey, 1861 (Condriichthyes: Carcharhinidae) na plataforma continental do estado do Maranhão, Brasil* (Vol. 13, pp. 51–65). São Luís, MA: *Boletim do Laboratório de Hidrobiologia*.
- Martínez, C. F., Salazar, C. Z., Böhm, G. S., Mendieta, J. C. V., & Estrada, C. M. (1985). *Efectos del fenómeno El Niño 1982-1983 sobre los principales recursos pelágicos y su pesquería (Arica-Antofagasta)* (Vol. 32, pp. 129–139). Santiago: *Investigación Pesquera (Chile)*.
- Motta, F. S., Gadig, O. B. F., Namora, R. C., & Braga, F. M. S. (2005). Size and sex compositions, length–weight relationship and occurrence of the Brazilian sharpnose shark, *Rhizoprionodon lalandii*, caught by artisanal fishery from southeastern Brazil. *Fisheries Research*, 74, 116–126.
- Motta, F. S., Namora, R. C., Gadig, O. B. F., & Braga, F. M. S. (2007). Reproductive biology of the Brazilian sharpnose shark (*Rhizoprionodon lalandii*) from southeastern Brasil. *ICES Journal of Marine Science*, 64, 1829–1835.
- Motta, F. S., Caltabellotta, F. P., Namora, R. C., & Gadig, O. B. F. (2014). Length–weight relationships of sharks caught by artisanal fisheries from southeastern Brazil. *Journal of Applied Ichthyology*, 30, 239–240.
- Oddone, M. C., & Amorim, A. F. d. (2007). Length–weight relationships, condition and population structure of the genus *Atlantoraja* (Elasmobranchii, Rajidae, Arhynchobatinae) in southeastern Brazilian waters, SW Atlantic Ocean. *Journal of Northwest Atlantic Fishery Science*, 38, 43–52.
- Paes, E. T., & Moraes, L. E. S. (2007). A new hypothesis on the influence of the El Niño/La Niña upon the biological productivity, ecology and fisheries of the Southern Brazilian bight. *Pan-American Journal of Aquatic Sciences*, 2(2), 94–102.
- Parsons, G. R., & Hoffmayer, E. R. (2005). Seasonal changes in the distribution and relative abundance of the Atlantic Sharpnose shark *Rhizoprionodon terraenovae* in the North Central Gulf of Mexico. *Copeia*, 2005(4), 914–920.
- Parsons, G. R., Hoffmayer, E. R., Frank, J., & Bet-Sayad, W. (2007). A review of shark reproductive ecology: Life history and evolutionary implications. In M. J. Rocha, A. Aruke, & B. G. Kapoor (Eds.), *Fish reproduction* (pp. 435–469). Boca Raton, FL: Taylor and Francis.
- Peres, M. B., & Vooren, C. M. (1991). Sexual development, reproductive cycle and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. *Fishery Bulletin*, 89, 655–667.
- Pethybridge, H. R., Parrish, C. C., Bruce, B. D., Young, J. W., & Nichols, P. D. (2014). Lipid, fatty acid and energy density profiles of white sharks: Insights into the feeding ecology and Ecophysiology of a complex top predator. *PLoS One*, 9(5), e97877. <https://doi.org/10.1371/journal.pone.0097877>
- Rochowski, B. E. A., Walker, T. I., & Day, R. W. (2015). Geographical variability in life-history traits of a midslope dogfish: The brier shark *Deania calcea*. *Journal of Fish Biology*, 87, 728–747.
- Santander, H., & Zuzunaga, J. (1984). Cambios en algunos componentes del ecosistema marino frente al Perú durante el fenómeno El Niño 1982-1983. *Revista de la Comisión Permanente del Pacífico Sur*, 15, 311–331.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Corso JT, Gadig OBF, Barreto RRP, Motta FS. Condition analysis of the Brazilian sharpnose shark *Rhizoprionodon lalandii*: evidence of maternal investment for initial post-natal life. *J Fish Biol.* 2018;93:1038–1045. <https://doi.org/10.1111/jfb.13780>