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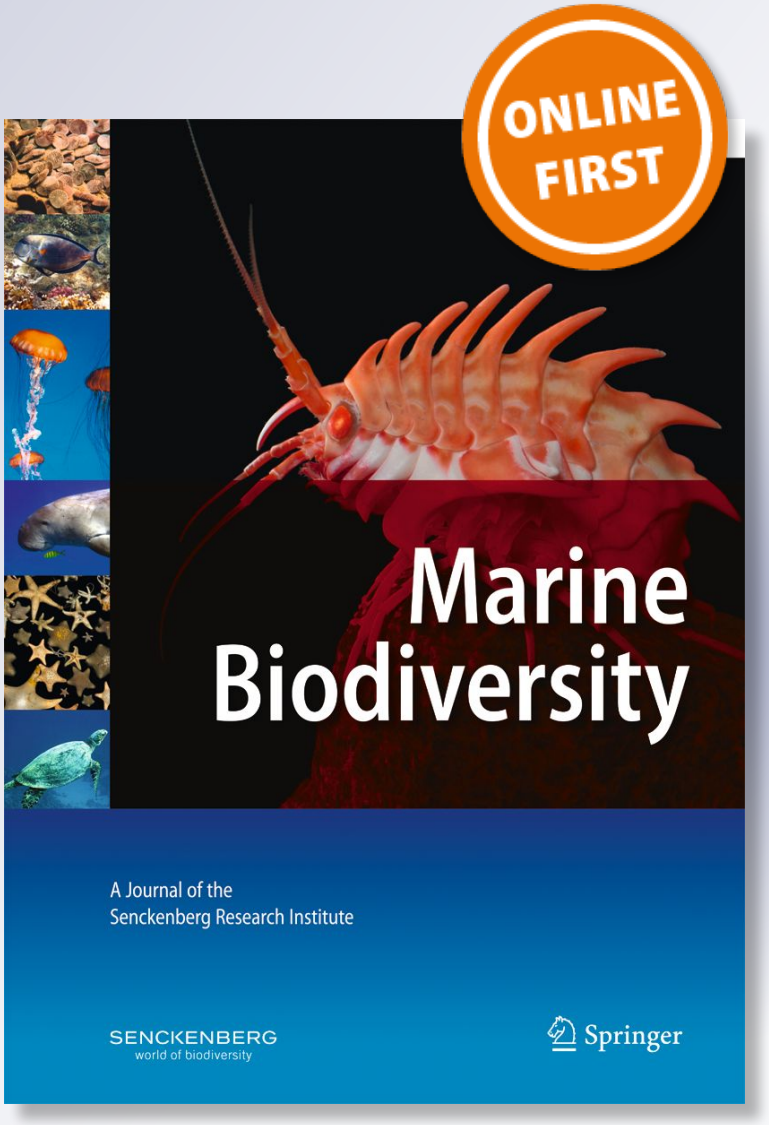

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Analysis of the morphological variation of *Doryteuthis sanpaulensis* (Cephalopoda: Loliginidae) in Argentinian and Brazilian coastal waters using geometric morphometrics techniques

Ramiro Braga[1] · **Augusto César Crespi-Abril**[2,3,4] · **Silvina Van der Molen**[1] · **Mara Cristiane Rodrigues Silveira Bainy**[5] · **Nicolás Ortiz**[1,6]

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Abstract Shape variation of individuals from three locations, two from Argentina and one from Brazil, was analysed by geometric morphometrics techniques. Individuals were weighed, measured, sexed, assigned to a maturity stage and photographed. For the analysis, two landmark configurations were used: one of nine landmarks (9L) and another of 25 landmarks (25L). To visualise shape variation, a principal component analysis (PCA) on Procrustes coordinates was conducted. The percentage of total shape variation explained by the 9L configuration was 80.5% (PC1: 61% and PC2: 19.5%), while the percentage for the 25L configuration was 76.4% (PC1: 54.8% and PC2: 21.6%). Based on this, shape analyses were performed using only the 9L configuration. The PCA results indicated that specimens show a large overlap between the categories based on sex and maturity stage. When location is considered, squid shape from São Sebastião and Rawson Port were very similar, while in Nuevo Gulf, the presence of two different morphological groups were observed: one similar to São Sebastião and Rawson Port, and the other with a morphology typical of Nuevo Gulf. Thus, two different morphotypes were defined: (i) morphotype of the continental shelf and (ii) morphotype typical of the gulf. The continental shelf morphotype is characterised by larger fins and wider mantle than the gulf morphotype. These results suggest that the morphotypes of *Doryteuthis sanpaulensis* are adaptations to oceanographic regimens.

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Keywords Phenotypic variation · Southern Atlantic Ocean · Ontogenetic shape variation · Interpopulation shape variation

Introduction

Some biological aspects, such as the timing of life cycle, location of spawning areas, different individual growth rates and different morphology, lead to the formation of intraspecific groups (Nigmatullin et al. 2001; Laptikhovsky et al. 2001; Boyle and Rodhouse 2005; Rodhouse et al. 2014). In cephalopods, the study of the intraspecific groups' characteristics is important to understand the population structuring of the species and to implement management strategies of fishing resources (Rabinovich 1978; Boyle 1990; Lipiński et al. 1998). The main techniques used to identify intraspecific groups are natural markers (e.g. parasites, otoliths isotopic composition and fatty acid profiles in tissues), genetic analysis (e.g. chromosomal morphology, molecular techniques),

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artificial markers (e.g. internal or external tags) and morphological analysis (e.g. traditional, geometrical) (Cadrin 2000).

The traditional morphometrics studies are based on the relation between linear dimensions taken between two anatomical points to describe the morphology of the specimens. This approach has several disadvantages, including the loss of information by simplifying the shape of the individuals and the fact of selecting a dimension which may not capture the shape variation clearly (Bookstein 1998). To avoid these constrains, an alternative technique based on the analysis of landmark coordinates and including the study of the shape in a two- or three-dimensional space was developed: geometric morphometrics (GM) (Toro Ibacache et al. 2010; Adams et al. 2004). This technique allows investigating the morphological changes of the structure of interest, considering the global anatomic context and avoiding the loss of information by the simplification of specimens shape (Richtsmeier et al. 2002). Despite its advantages, the use of GM in cephalopods has been restricted only to the study of the ontogenetic variation of the body and lower beak of the squid *Illex argentinus* in two spawning groups (Crespi-Abril et al. 2010), and to the analysis of intra- and interspecific variation of the sepion shape in three different cuttlefish species: *Sepia officinalis*, *S. elegans* and *S. orbignyana* (Neige and Boletzky 1997).

Loliginid squids play a significant economic and ecological role in worldwide coastal marine ecosystems, as many species are fishery resources and represent a key link in marine food webs (Pierce and Guerra 1994; dos Santos and Haimovici 2002; Boyle and Rodhouse 2005; De Pierrepont et al. 2005; Rodhouse 2005). The loliginid squid, *Doryteuthis sanpaulensis*, is present in the Brazilian, Uruguayan and Argentinian shelf from 23°S to 46°S between coastal and shelf waters (Brunetti et al. 1999; Vidal et al. 2013). This species is not the target of an industrial fishery but is captured as bycatch in bottom trawl fisheries (i.e. *Pleoticus muelleri*, *Artemesia longinaris* and *Merluccius hubbsi*) and other squid fisheries (*I. argentinus* and *D. plei*), as bycatch of pink-shrimp trawl fishery (*Farfantepenaeus* spp.) and in recreational fisheries along the Argentinian coast (Brunetti et al. 1999; Rodrigues and Gasalla 2008). Several studies were conducted to describe the biological characteristics of this species along its distribution range (Vigliano 1985; Costa and Fernandes 1993; Pineda et al. 1998, 2002; Brunetti et al. 1999; Barón 2001a, b; Barón and Ré 2002a, b; Garri and Ré 2002; Martins and Perez 2007; Rodrigues and Gasalla 2008; Crespi-Abril et al. 2014) but studies which aimed to determine the population structure of the species are scarce and outdated (i.e. Juanicó 1983). In this paper, we studied the morphology of *D. sanpaulensis* using GM and compared the shape variation between different locations along the geographical distribution range of the species.

Materials and methods

Study areas and specimen sampling

Individuals were obtained between February 2014 and April 2014 from three different locations along the geographical distribution range of the species: Nuevo Gulf (Argentina), Rawson Port (Argentina) and São Sebastião (Brazil) (Fig. 1).

In Nuevo Gulf, 65 specimens were captured at Luis Piedra Buena dock during the night using jigs (Table 1). This gulf is a semi-enclosed basin with an average depth of 80 m and a maximum depth of 180 m (Rivas and Beier 1990), and it is communicated to the adjacent shelf through an opening 16 km wide. The opening is relatively narrow and it limits substantially the circulation and exchange of water with the adjacent platform (Rivas and Beier 1990). Therefore, the currents inside the gulf are weak (1– 4.5 cm s^{-1}) and mainly driven by wind stress (Palma et al. 2008; Tonini et al. 2013). The temperature in the water column varies depending on the time of the year (Rivas 1990; Rivas and Beier 1990; Dellatorre et al. 2012): there is a strong stratification during summer with temperatures of 18 °C at surface and 11 °C at the bottom, while in winter, the gulf waters are thermally homogeneous, with an average temperature of 10.25 °C (Rivas 1990; Rivas and Beier 1990; Dellatorre et al. 2012).

In Rawson Port, 33 specimens were captured as bycatch of shrimp (*Pleoticus muelleri*) bottom trawlers. The fishing area is located in near shore waters between 43°20′ and 43°32′S, from the coast to 24 km offshore. The water column is homogeneous, with an average temperature between 10 and 11 °C during winter and between 16 and 17 °C during summer (Ruiz and Mendia 2008).

In São Sebastião, 22 specimens were obtained as bycatch of pink-shrimp trawl fishing (*Farfantepenaeus* spp.). This region is characterised by having a maximum depth of 50 m and the water temperature ranges from 17 °C in winter to 31 °C in summer. The area is influenced by three water masses, coast water, tropical water and South Atlantic Central Water, and their distribution and seasonal variation are typical of the southeastern shelf (Matsuura 1986; Castro Filho et al. 1987; Migotto and Vervoort 1996).

The last two sites (Rawson Port and São Sebastião) have stronger currents compared to Nuevo Gulf, since they are directly exposed to shelf-water influence. The current values estimated in the Argentinian and Brazilian shelf range from 5 to 10 cm s^{-1} (Lima et al. 1996; Soares and Möller 2001; Palma et al. 2008; Tonini et al. 2013).

To avoid bias due to manipulation by different researchers, a standardised protocol for specimen processing and image acquisition was applied in the three locations. Specimens were preserved chilled and processed in the laboratory. Each individual was photographed with a Sony DSC-W70 7.2-megapixel digital camera and the dorsal mantle length (DML), total

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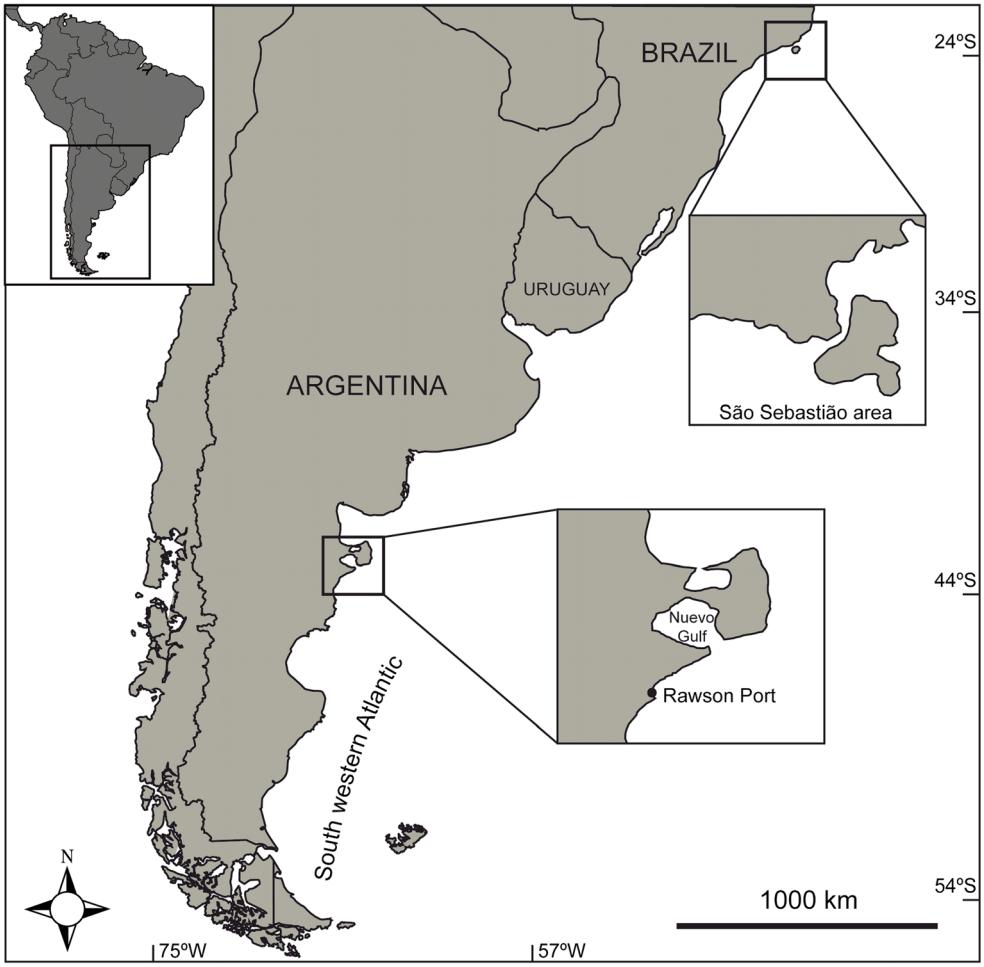

Fig. 1 Study area indicating the locations where individuals of *Doryteuthis sanpaulensis* were collected: São Sebastião, São Paulo, Brazil; Nuevo Gulf, Argentina; and Rawson Port, Argentina

weight (TW), sex and maturity condition based on the macroscopic characteristics of the reproductive system were recorded (Barón and Ré 2002b) (Table 1).

Photographs were taken with the ventral part of the mantle facing the camera and the dorsal part supported on a rigid platform to prevent fins deformation (Fig. 2). The specimens were digitalised using the software tpsDig2 (Bookstein 1998).

Two different landmark configurations were used: one of nine landmarks (9L) and another of 25 landmarks (25L). According Dryden and Mardia (1998), a homologous landmark is a point of correspondence on each object that matches between and within populations. The 9L configuration was suggested by Crespi-Abril et al. (2010) and is conformed only by anatomical landmarks. The 25L configuration was implemented in this study in order to improve accuracy. This configuration is conformed by nine landmarks (the same as in the 9L configuration) and 16 semi-landmarks (Fig. 2). To correct any bending in the body of the squid, the 'unbend specimens' function from tpsUtil software was implemented (Rohlf 2016). This function forces the alignment of the landmarks on the longitudinal axis and modifies the position of the rest of the landmarks of the configuration consequently. For the 9L configuration, the landmarks considered in the longitudinal axis were 8, 9 and 4, and for the 25L configuration 20, 21 and 10 (Fig. 2). Translation, rotation and scale effects were removed by means of a generalised Procrustes analysis (GPA)

Table 1 Number of specimens obtained at each location

Location	Males			Females			Total number of samples
	Immature	Maturing	Mature	Immature	Maturing	Mature	
Nuevo Gulf	20	22	13	8	2	0	65
Rawson Port	1	2	3	18	3	6	33
São Sebastião	3	9	1	1	8	0	22

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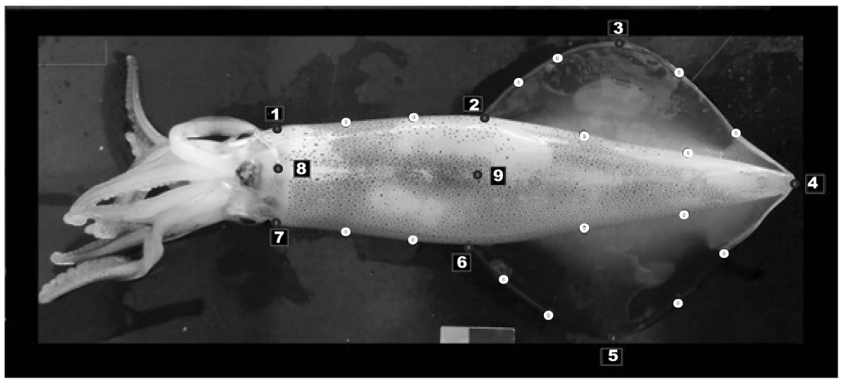

Fig. 2 Landmarks placement on *Doryteuthis sanpaulensis* mantle and fins. The *grey points* are anatomical landmarks and the *white points* are semi-landmarks

(Adams et al. 2004; Zelditch et al. 1998). In this method, landmark configurations are superimposed by least squares optimisation and the process is iterated to compute the mean shape (Adams et al. 2004; Zelditch et al. 2004). After GPA, shape differences can be analysed by the differences between Procrustes coordinates. Centroid size (CS), which is calculated as the square root of the sum of the squared deviations of landmarks from a centroid (Bookstein 1991; Zelditch et al. 2004) for each specimen, was used as a size proxy. The presence of allometry (changes in shape related to changes in size) was examined by a multivariate regression analysis between shape scores as a dependent variable (Procrustes coordinates) and size as an independent variable (CS). The main tendencies in shape variation between specimens within samples were summarised through a principal component analysis (PCA) of the variance–covariance matrix of the Procrustes coordinates. All shape analyses were performed using MorphoJ v1.05d (Klingenberg 2011). More details of the framework of GM using landmarks can be found in Zelditch et al. (2004).

Additionally, to analyse ontogenetic shape variation of the mantle, a dispersion graphic was built between the first principal component and the DML, as suggested by Crespi-Abril et al. (2010).

Results

The multivariate regression of shape on CS was significant (permutation test with 10,000 random permutations, $p < 0.017$). Consequently, subsequent analyses were performed with the residuals of the regression, which are free of allometric effects.

According to the PCA, the percentage of total variation of the shape explained by the 9L configuration was 80.5% (PC1: 61% and PC2: 19.5%), while the percentage of total variation for the 25L configuration was 76.4% (PC1: 54.8% and PC2: 21.6%). Thus, further analysis of shape variation was performed based on the 9L configuration, which explained a higher percentage of the total variance compared to the 25L configuration.

The PCA results indicated that specimens show a large overlap between the categories based on sex (Fig. 3b) and maturity stage (results not shown). When the location is considered, the squid shape from São Sebastião and Rawson Port were very similar, while in Nuevo Gulf the presence of two different morphological groups were observed (Fig. 3a). The specimens shape of one of these groups is more similar to the São Sebastião and Rawson Port shapes than to the second group of the same location, while the other group shows a morphology only observed in specimens from Nuevo Gulf. Based on these results, specimens were regrouped and two different morphotypes were defined: (i) a morphotype of the continental shelf conformed by specimens of São Sebastião, Rawson Port and Nuevo Gulf (represented by PC1 negative values) and (ii) a morphotype typical of the gulf, conformed only by specimens of Nuevo Gulf (represented by PC1 positive values). The shape of the continental shelf morphotype is characterised by a more robust body (larger fins and wider mantle) than the gulf morphotype (Fig. 3a).

Both morphotypes' specimen size was similar and ranged from 60 to 230 mm of the DML. Figure 4 shows that both morphotypes presented the same tendency of ontogenetic shape variation: as individuals grow, fins become larger and the mantle becomes wider (Fig. 4). Regarding the ontogenetic variation, it was noted that both morphotypes showed the same trend.

Discussion

Despite the fact that GM techniques have been widely used to detect subtle shape variations that can be missed when traditional morphometry is used (Bookstein 1998; Zelditch et al. 1998; Adams et al. 2004), in cephalopods, the application of these methods is rare. Probably, the main factor limiting the use of GM techniques in this class is the difficulty in placing homologous landmarks on firm anatomical structures. This is particularly noticeable in the soft body of the order Octopoda. Conversely, in the orders Sepiida, Teuthida, and Nautilida, GM techniques have the potential to be implemented, since

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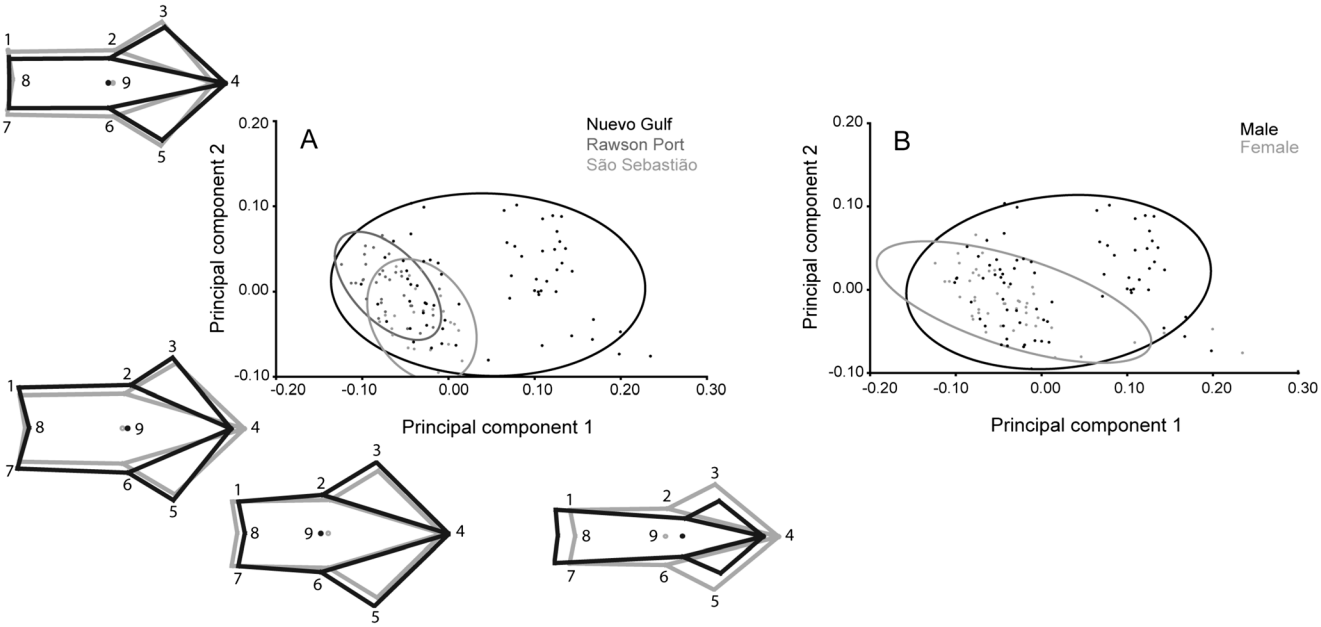

Fig. 3 Principal component analysis (PCA; PC1 61% and PC2 19.5%) showing the total shape variation. Individuals are categorised by location (**a**) and sex (**b**). The ellipses enclose 95% of observations. The wireframes indicate shape changes along the axes: *grey lines* represent the mean shape and *black lines* correspond to the displacement of the landmarks at each axis extreme

these groups have a more solid body, given by the presence of rigid structures, such as sepion/gladius or shell. For example, Neige and Boletzky (1997) determined inter- and intraspecific shape variations between *S. officinalis*, *S. elegans* and *S. orbignyana* using a landmarks configuration in the sepion and Crespi-Abril et al. (2010) analysed the shape variation between two spawning groups of *I. argentinus* using a configuration of homologous landmarks in the mantle, fins and lower beak.

In *D. sanpaulensis*, two landmark configurations were implemented to compare fins and mantle shape variation. The 9L configuration explained a higher percentage of the total shape variation in relation to the 25L configuration, despite being a configuration with fewer points to describe the mantle and fins shape. The 25L configuration is conformed by 16 additional semi-landmarks with respect to the 9L configuration. Semi-landmarks are not positioned at anatomical points but they are placed on the contour of the mantle between landmarks (Fig. 2) and then slid so as to minimise the bending energy during GPA (Bookstein 1997). These additional points showed a high dispersion around the mean shape, which leads to a decrease in the percentage of the total variation explained by PCA. Therefore, the 9L configuration represents the most appropriate configuration to characterise *D. sanpaulensis* mantle and fins shape.

As a general pattern, since female gonads are bigger than male gonads, the most notorious sexual dimorphism trait in squids corresponds to females being larger and heavier than males when they reach the maximum maturity stage (Rodhouse and Hatfield 1992; Belcari 1996; Boyle and Rodhouse 2005). In *D. sanpaulensis*, this same pattern was observed between 23°S and 44°S (Vigliano 1985; Costa and Fernandes 1993; Barón and Ré 2002a, b). In the present study, no sexual dimorphism was observed: males and females of

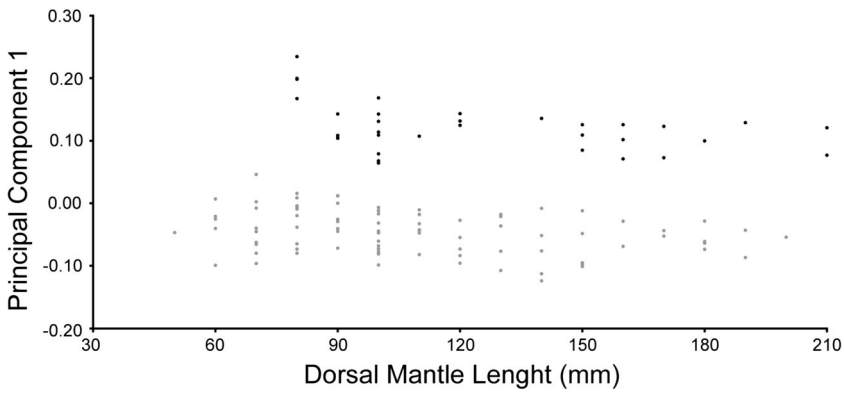

Fig. 4 Shape variation (PC1) as a function of the dorsal mantle length (DML, mm) for both morphotypes. The *black points* represent individuals belonging to the morphotype of the gulf and the *grey points* represent individuals belonging to the morphotype of the continental shelf

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D. sanpaulensis presented a similar mantle and fins shape. Additionally, shape did not vary between the maturity condition of individuals. A similar result was reported for *I. argentinus* captured on the Argentinian coastal waters (Crespi-Abril et al. 2010).

Cephalopods present a high phenotypic plasticity, mainly influenced by environmental factors and food availability (Boyle and Boletzky 1996; Hatfield et al. 2001; Boyle and Rodhouse 2005; Sinn et al. 2008). This plasticity may be the cause of phenotypic intrapopulation groups (Boyle and Rodhouse 2005; Crespi-Abril et al. 2010). Particularly in loliginid squids, phenotypic intrapopulations groups have been observed in several studies. For example, the analysis of morphometrics data in the Northeast Atlantic Ocean has shown differences between *Loligo forbesii* from the continental shelf compared to those of overseas (Pierce et al. 1994). In the Southwest Atlantic Ocean (8°S to 27°S), Zaleski et al. (2012) distinguished local morphotypes in *Lolliguncula brevis* and suggest that exclusive phenotypes can be maintained in relatively small and enclosed areas, such as bays and estuaries. In the Southeast Atlantic Ocean, for *Loligo reynaudii*, Van Der Vyver et al. (2015) suggested environmental heterogeneity as the primary driver of the observed phenotypic divergence. Furthermore, Juanicó (1983) observed that, in *D. sanpaulensis*, two morphologically similar groups were separated by a different one (28°S to 30°S) in the Southwest Atlantic Ocean (23°S to 38°S). One of the most studied factors influencing phenotypic plasticity is water temperature (Forsythe 1993; Pierce et al. 1994; Hatfield 2000; Forsythe et al. 2001): it is expected that individuals which experience different thermal history will present differences in some biological parameters (e.g. individual growth rate, maximum size, size at maturity). However, our results suggested that temperature is not the main factor influencing *D. sanpaulensis* shape variation, since individuals from Brazilian waters were similar to individuals from Argentinian waters, despite the differences in water temperature.

In the present study, two morphotypes were distinguished: the gulf and shelf morphotypes. The specimens with the gulf morphotype were characterised by fins and mantle narrower than the shelf morphotype specimens. In this sense, a more robust mantle and fins are expected to increase the swimming capacity and to reduce the locomotion costs of individuals (O'Dor 1988; Zaleski et al. 2012). Considering that Nuevo Gulf is a semi-enclosed basin with weaker currents (<5 cm s^{-1}, mainly driven by wind stress) than the much more dynamic shelf waters (Palma et al. 2008; Tonini et al. 2013), the two morphotypes detected may be influenced by differences in water dynamics at each location. However, in Nuevo Gulf, both morphotypes coexist. This could be explained by the fact that some individuals complete their life cycle inside the gulf (Barón 2001a, b), developing a similar body shape to the gulf morphotype ones, while other individuals complete their life cycle in shelf waters, developing the shelf morphotype and migrate into coastal waters (including Nuevo Gulf) to spawn (Barón and Ré 2002b).

Squids usually show marked ontogenetic changes in fins and mantle shape as individuals pass from paralarvae to adults with higher swimming capacity, linked to intense reproductive migrations and to active predatory behaviour (Boyle and Rodhouse 2005). Our analysis of the shape ontogenetic variation in *D. sanpaulensis* revealed that both morphotypes showed the same trend: an increase in the relative size of the fins and the width of the mantle as specimens grow. Therefore, these results would show that individuals of *D. sanpaulensis* develop greater swimming capacities as they grow, regardless of the environment in which they inhabit.

Morphological diversity is the product of genetic, developmental and environmental influences. Shape variation may indicate different functional roles, different responses to selective pressures, as well as differences in life history traits. Shape analysis is one approach to understanding these diverse causes of variation (Zelditch et al. 2004). The results presented in this study revealed the presence of two morphotypes in *D. sanpaulensis*. These differences are not associated with the latitudinal range, since groups of closest sites are more dissimilar than groups separated for more than 20° of latitude. In agreement with Juanicó (1983), this suggests that the population structure of *D. sanpaulensis* may be complex and different morphotypes are probably adapted to different hydrodynamic regimes.

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