Description and quantitative analysis of the dentition of the southern thorny skate *Amblyraja doellojuradoi*

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A description of the tooth morphology of 234 jaws from the southern thorny skate *Amblyraja doellojuradoi* in the south-west Atlantic Ocean is given. Seven rows of teeth were selected and length and width of each tooth in these rows were measured. It was found that functional series corresponds to the third teeth and the average width and length of these teeth were compared among jaws, maturity stages, sexes and rows. Generalized linear models were used to determine the subset of measures that most contribute to explain the variability between groups. It was observed that males have longer teeth than females, but the teeth of females are wider. These differences are attributed to reproductive behaviour, in which males bite females to hold them during copulation. This study provides a description of the teeth of *A. doellojuradoi*, supplying a valuable tool for identification of species. In addition, the establishment of the main variations observed in the dentition, improves the understanding of the species' biology.

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Key words: generalized linear models; Rajidae; tooth morphology.

INTRODUCTION

The study of teeth in cartilaginous fishes is a very important tool for determining species, establishing phylogenetic relationships of living and extinct taxa and describing ontogenetic morphological changes (Sáez & Lamilla, 2004). Elasmobranch teeth are replaced during ontogeny (Kemp, 1999), maintaining a dentition according to all stages of growth (Moss, 1972). Through wear, those of the following posterior rows replace many teeth of the outer rows of the jaw (Moss, 1972). Germinal teeth appear in the germinal area displacing the functional series outwards (Becker *et al.*, 2000).

Chondrichthyan teeth show a variety of shapes or sizes and play different roles during catching and handling prey (Applegate, 1965). Several studies have demonstrated the relationship between tooth shape and function. Piscivorous species have tall, narrow teeth, whereas species that feed on marine mammals and reptiles have large, serrated teeth, and species that feed on crabs, molluscs and other hard-shelled organisms have a

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mosaic dentition (Budker, 1971; Lagler *et al.*, 1977; Cailliet *et al.*, 1986; Tricas *et al.*, 1997). McEachran *et al.* (1976) found variations in the shape of the mouth and stated that the number of rows of teeth was related to the feeding habits of each species. Sexual and ontogenetic dimorphism, however, had also been described and some differences were found in the number and arrangement of teeth between jaws (Leible, 1988; Herman *et al.*, 1996; Kajiura & Tricas, 1996; Rivera, 2009; Shimabukuro, 2009; Gutteridge & Bennett, 2014). Furthermore, sexual dimorphism has been related with the bite of males to immobilize females during mating (Pratt & Carrier, 2001).

Study of dental morphology of skates (Rajidae) has improved the understanding of various biological and taxonomic characteristics of batoids (Hubbs & Ishiyama, 1968; Du Buit, 1978; Miyake & McEachran, 1988; Herman *et al.*, 1995). Herman *et al.* (1994, 1995, 1996) conducted a thorough review of the tooth morphology of skates, describing and illustrating the dentition of 26 representative genera worldwide, allowing subsequent comparison with other species and subsequent analysis and interpretation of these variations. Of the 10 species that comprise the genus *Amblyraja* Malm 1877, only the dentition of the starry skate *Amblyraja radiata* (Donovan 1808) has been analysed in detail so far and few data on the dentition of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) and the Jensen's skate *Amblyraja jenseni* (Bigelow & Schroeder 1950) were published (Orlov & Cotton, 2011; Bustamante *et al.*, 2012). In the south-west Atlantic Ocean *Amblyraja doellojuradoi* (Pozzi 1935) is the most common species of its genus, but little is known of its biology so far. Only recently have there been analyses of its diet (Delpiani *et al.*, 2013), reproduction (Delpiani, 2016) and particular dental anomalies (Delpiani *et al.*, 2012). The last study includes a brief qualitative description of the dentition, finding that *A. doellojuradoi* has a gradient monognathic heterodonty. The aim of this paper is to provide a thorough analysis of the dentition of *A. doellojuradoi*, assessing sexual and ontogenetic differences.

MATERIALS AND METHODS

SAMPLING

The jaws from 234 *A. doellojuradoi* were analysed, corresponding to specimens collected during research cruises carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) ($n = 142$) and from commercial vessels ($n = 92$) between 2005 and 2012, in the south-west Atlantic Ocean between 36° 0′ and 52° 47′ S, from 75 to 414 m deep (Fig. 1). Total length (L_T) of each specimen was measured (mm) and its sex recorded. Maturity stages, *i.e.* juvenile or adult, were determined according to the degree of clasper calcification, development of testes and reproductive ducts in males and on the condition of uteri, oviductal glands and ovarian follicles in females (Stehmann, 2002). Jaws were extracted, cleaned and the dental plates were removed from the jaws and placed on vegetal paper. Symphyseal teeth of both sexes and maturity stages were selected for a detailed description of individual tooth morphology; these teeth were observed with an S.E.M. JSM-6460LV (accelerating voltage of 15 kV; JEOL; www.jeol.co .jp). For this, the samples were mounted on an aluminium disc and coated with gold by a metallization mark Denton Vacuum Desk II (www.dentonvacuum.com). Subsequently, photographs of the teeth from the image generated by the S.E.M. were taken.

QUANTITATIVE ANALYSIS

Tooth rows were counted and this number was plotted against L_T to evaluate whether they were correlated. A *t*-test was performed to assess whether there were significant differences in the number of rows between sexes, maturity stages and among the upper and lower jaws in
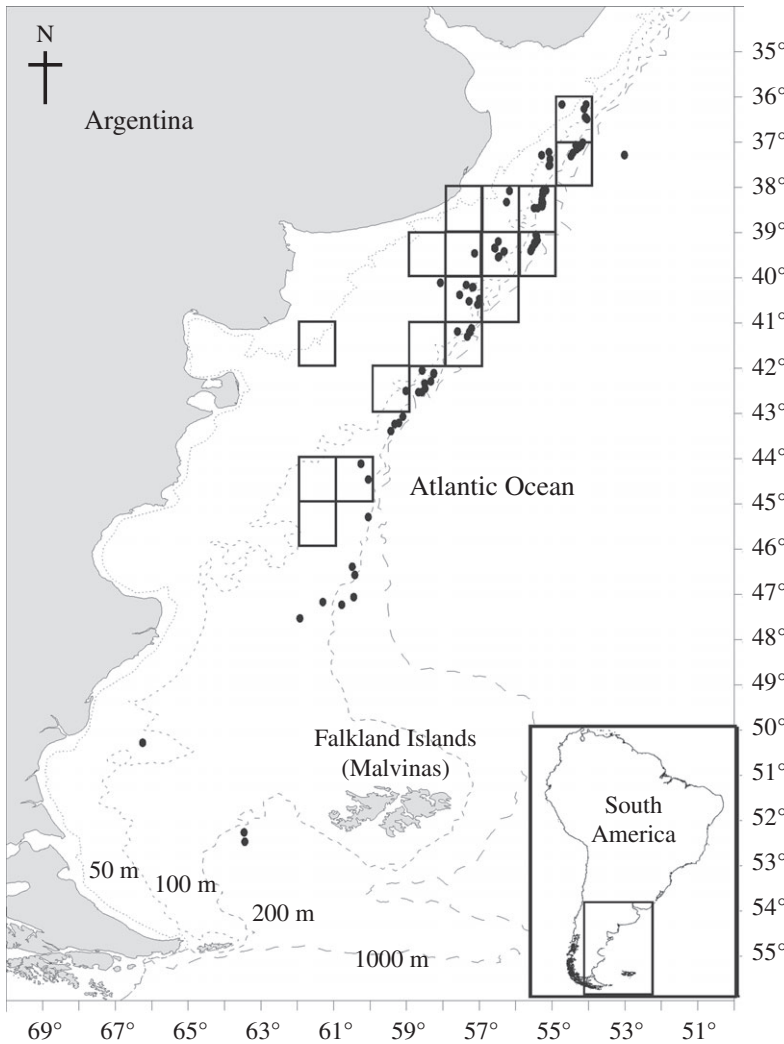
FIG. 1. Map of the study area, showing the location of fishing sets (●) and quadrant (□) where *Amblyraja doellojuradoi* was captured.

each sex (Mann–Whitney *U*-test was used when the assumptions of normality were not accomplished). All the statistical analyses were performed using the R statistical software, 2.13.0 (www.r-project.org).

Seven tooth rows of the upper and lower jaws were selected such that all areas, commissure, commissure region, symphysis region and symphysis were represented, as suggested by Rivera (2009). The following rows were considered for each hemi-mandible: C, the second row from the commissure; CR, the sixth row from the commissure; SR, the fifth row from the symphysis; S, the symphysis row, giving a total of seven selected rows (Fig. 2). The width and length of each tooth of these seven rows were measured according to Sáez & Lamilla (1997). The Mann–Whitney *U*-test was used to compare width and length of the selected rows of the right and left hemi-mandibles. Given that no differences were found, the right rows were used for the following analyses.
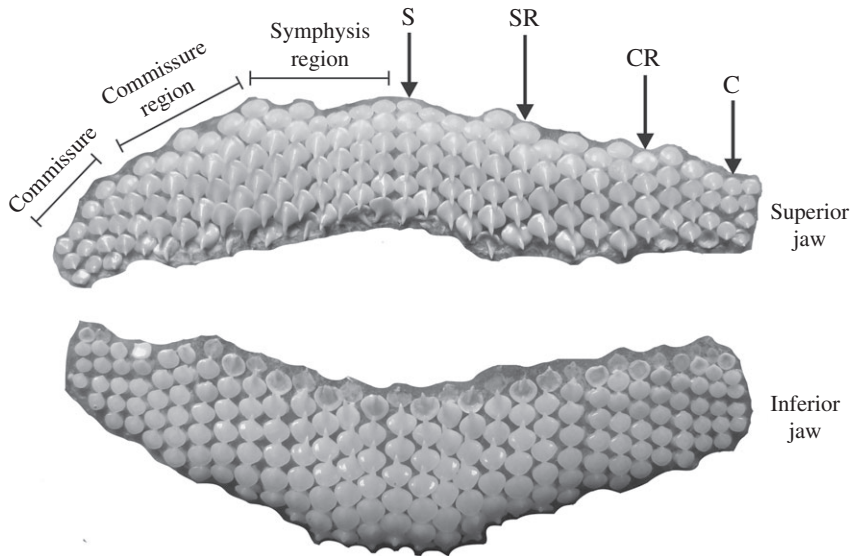
FIG. 2. Dental plates of an adult male *Amblyraja doellojuradoi*. The tooth rows and jaw region analysed are shown. S, symphysis row; SR, symphysis region row; CR, commissure region row; C, commissure row.

Average length and width of each selected tooth of both jaws for all groups of the seven selected rows was calculated and these values were compared among teeth of the same row using the Kruskal–Wallis test. When there were differences between the mean values of these teeth, Dunn's test was used to locate the difference. According to these results, the tooth number of the functional series was determined and used to compare among groups. The functional tooth was regarded as the first tooth having approximately the same length and width as the tooth that precedes it in the same row; that is, the oldest tooth of the row having no wear (Shimabukuro, 2009).

Generalized linear models (GLM; Venables & Ripley, 2002) were used to determine the sub-set of measures that contributed the most to explain variability among groups. Thus, for each group (upper width, upper length, lower width and lower length), the models were built with the length and width of the functional tooth as response variables, and sex, maturity stage and row as the independent variables. Models were also constructed with the combination of independent variables such as sex + maturity stage, sex + row, maturity stage + row and sex + maturity stage + row. Finally, a null model without any independent variable was constructed to test the hypothesis that none of the above has an effect on the response variable (Lucifora *et al.*, 2009). The model has a γ-error distribution due to the nature of the continuous dependent variable, with positive values and a log-link function (link $= \log_{10}$) (Zuur *et al.*, 2009). This multiple-hypothesis modelling approach was used to identify the model that best fits the data (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). For each model the AIC was calculated and the model with the lowest AIC was selected as the best model (Crawley, 2005). To obtain the likelihood of each competing model given the data, AIC weight (w) was calculated (Franklin *et al.*, 2001; Johnson & Omland, 2004).

RESULTS

QUALITATIVE ANALYSIS

The teeth of *A. doellojuradoi* (Fig. 3) are constituted by two main parts, the crown and the root. The crown has a marked cusp in both sexes, but those of mature males appear
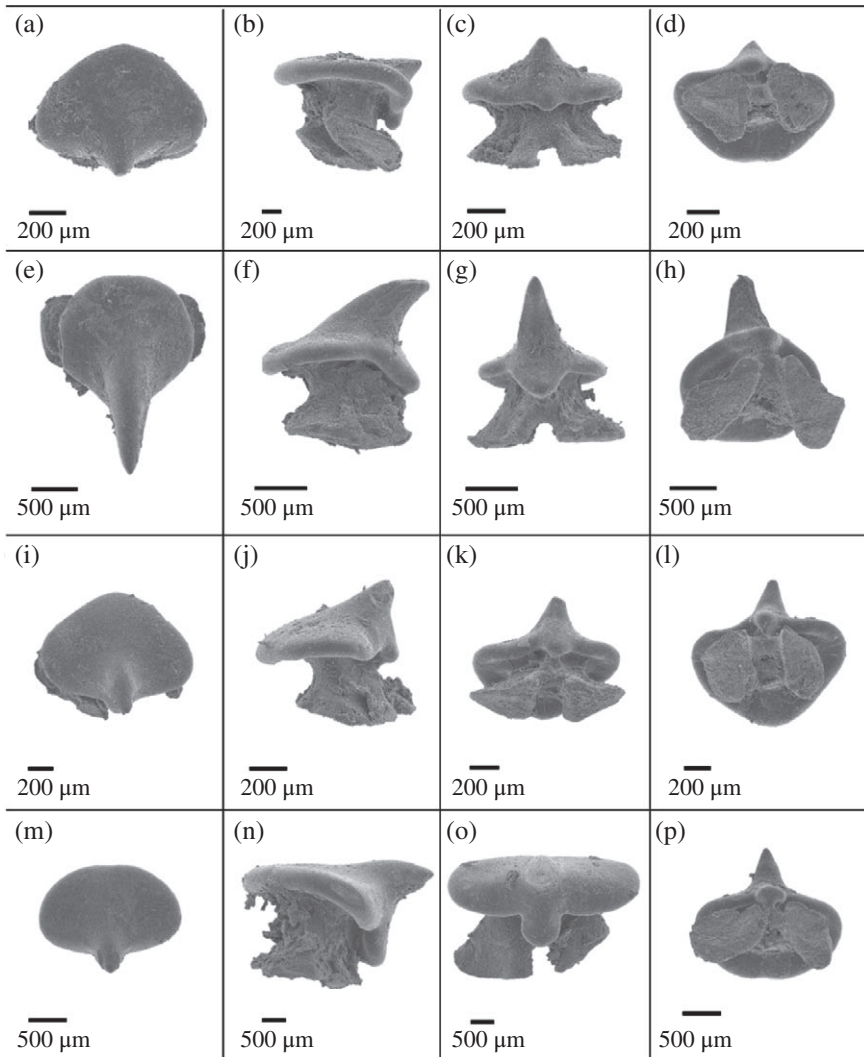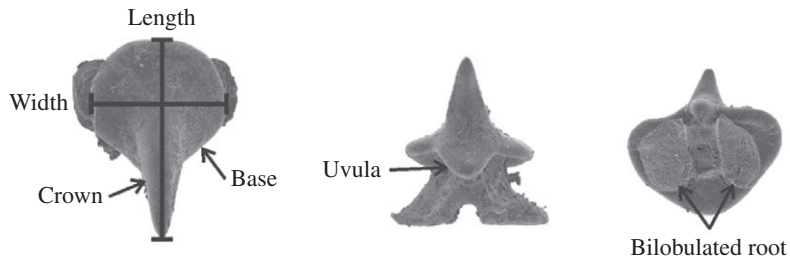
FIG. 3. Symphysial teeth of (a)–(d) immature males, (e)–(h) mature males, (i)–(l) immature females and (m)–(p) mature females of *Amblyraja doellojuradoi*. The first column shows the dorsal view of the tooth, the second shows a lateral view, the third shows the anterior view and the last shows the ventral view.

to be more erect and sharper than those of females and immature males. The base of the crown is triangular in immature specimens and round or oval in mature males and females, respectively. On the lingual and basal sides, rounded edges were observed. The basal surface of the crown has a unique ornamentation called uvula (lobed extension on the anterior part of the base) which is more evident in mature specimens. The stem of the root is oval in cross section and it divided into two by a transverse groove, creating a bilobulate root. Both sections of the root become distally wider in all directions, forming a large base with scalloped margins. In the middle of the transverse groove, at least two central foramina connect the outside with the inside of the tooth, where blood vessels penetrate the vascular channels of the pulp cavity; this type of vascularization is referred to as holaulacorhizid.

QUANTITATIVE ANALYSIS

In the upper jaws of males, the number of tooth rows varies from 26 to 37 (mean, $\bar{x} = 31 \cdot 2$) and in the lower ones it ranges from 24 to 35 ($\bar{x} = 30 \cdot 2$). In females the number of rows varies from 24 to 35 ($\bar{x} = 31 \cdot 4$) and 28 to 34 ($\bar{x} = 30 \cdot 6$) in the upper and lower jaws, respectively. There is no correlation between the L_T and the number of tooth rows in the upper jaw (Spearman correlation $= 0 \cdot 0006$; $n = 131$; 95% C.I. $= 27 \cdot 6 - 33 \cdot 85$; $P > 0 \cdot 05$) or in the lower jaw (Spearman correlation $= 0 \cdot 0011$; $n = 131$; 95% C.I. $= 26 \cdot 5 - 32 \cdot 71$; $P > 0 \cdot 05$) of males [Fig. 4(a), (b)] and neither in the upper (Spearman correlation $= 0 \cdot 0234$; $n = 101$; 95% C.I. $= 24 \cdot 87 - 32 \cdot 56$; $P > 0 \cdot 05$) nor the lower (Spearman correlation $= 0 \cdot 0009$; $n = 101$; 95% C.I. $= 28 \cdot 56 - 35 \cdot 29$; $P > 0 \cdot 05$) jaws of females [Fig. 4(c), (d)]. No significant differences were found in the number of rows between males and females, either in the upper jaw (Mann–Whitney U-test, $U = 7237 \cdot 5$; d.f. $= 231$; $P > 0 \cdot 05$) or in the lower jaw (Mann–Whitney U-test, $U = 7238 \cdot 5$; d.f. $= 238$; $P > 0 \cdot 05$). The number of rows between immature and mature males in the upper jaw ($t = -0 \cdot 55$; number mature $= 121$; number immature $= 21$; d.f. $= 26$; $P > 0 \cdot 05$) or in the lower jaw ($t = -0 \cdot 01$; number mature $= 121$; number immature $= 21$; d.f. $= 28$; $P > 0 \cdot 05$), and of immature and mature females in the upper jaw ($t = 1 \cdot 48$; number mature $= 83$; number immature $= 24$; d.f. $= 42$; $P > 0 \cdot 05$) and in the lower jaw ($t = -0 \cdot 18$; n number mature $= 83$; number immature $= 24$; d.f. $= 42$; $P > 0 \cdot 05$). Significant differences between the number of rows from the upper and lower jaw in males ($t = 3 \cdot 67$; $n = 142$; d.f. $= 239$; $P < 0 \cdot 001$) or females ($t = 3 \cdot 55$; $n = 107$; d.f. $= 162$; $P < 0 \cdot 001$) were found, with more rows in the upper jaw in the both sexes.

Measurements of the teeth of each row of the upper jaw in both sexes clearly show that teeth increase their width and length from the commissure row to the symphysis region, but decrease in the symphysis row itself (Fig. 5). In the lower jaw of both sexes a gradual increase of the width and length of teeth from the commissure to the symphysis was observed, showing the greatest width and length at the symphysis (Fig. 6).

The average width of the teeth of the same row remains constant from external to internal teeth in the four groups (immature male, mature male, immature female and mature female) for both jaws. The average length of the teeth of each row is significantly different between them, particularly in the teeth of the symphysis row (Table I). The third tooth of each row was used for comparisons among the four groups and between the selected rows along the jaw, because it would be involved in the apprehension (functional teeth).
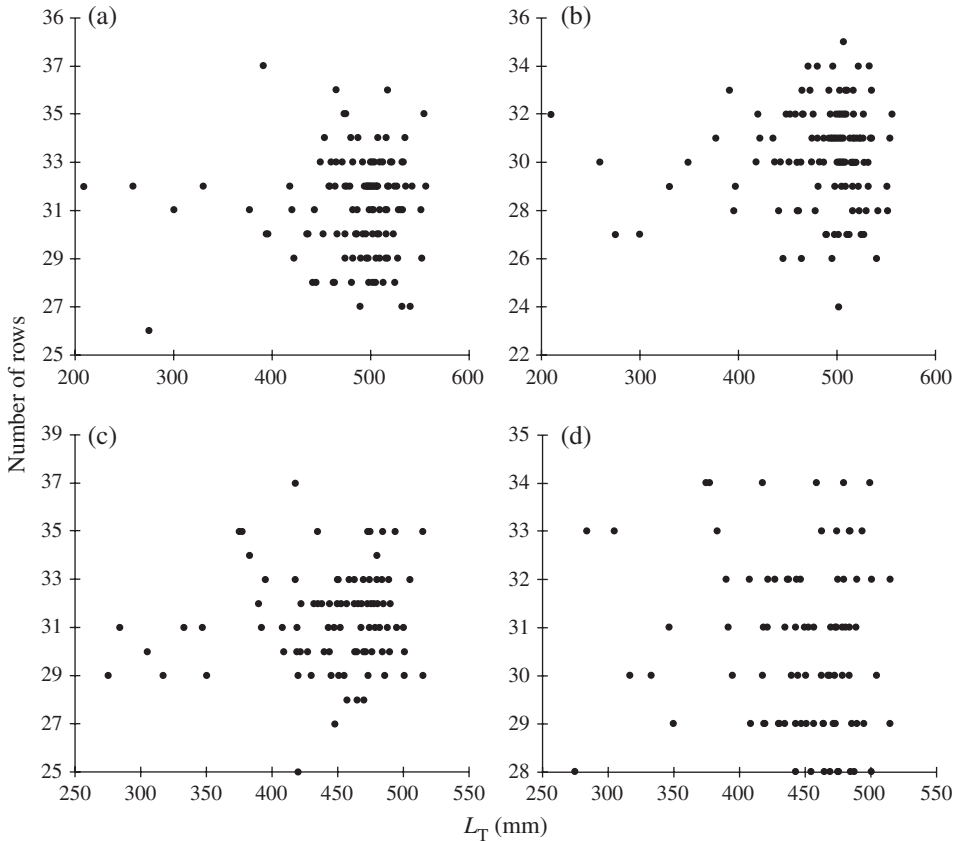
FIG. 4. Correlation between the total length (L_T) and the number of tooth rows in the (a) upper ($r^2 = 0.0005$, $P > 0.05$) and (b) lower ($r^2 = 0.0011$, $P > 0.05$) jaw of males, and (c) in the upper ($r^2 = 0.0189$, $P > 0.05$), and (d) lower ($r^2 = 0.0065$, $P > 0.05$) jaw of females of *Amblyraja doellojuradoi*.

The width and length of the teeth varies according to sex, the maturation stages of the specimens and depending on the row to which they belong (Table II). The model that best explains the variation in tooth width of both jaws (upper and lower) is the one that combines sex and rows; the model which best explains the variation of the length of the teeth from both jaws is the one that combines all variables (sex, maturity stage and rows). In the upper and in the lower jaw, it was observed that females' teeth are wider than those of males and the teeth of mature males are longer compared with immature males and all females (Table II). The tooth bases of females tend to be horizontally oval, whereas they are rather circular in males. Thus, the rows in males are more separated and defined than in females. Furthermore, in the upper jaw, tooth width and length varies among rows, with the widest and longest teeth in the row of the symphysis region, then the commissure region, the symphysis row and finally the commissure, which has narrower and shorter teeth (Table II). Also, in the lower jaw, both tooth width and length vary among rows, being of greater width and length for the teeth in the symphysis row, followed by the region of the symphysis, the region of the commissure and finally those corresponding to the commissure (Table II).
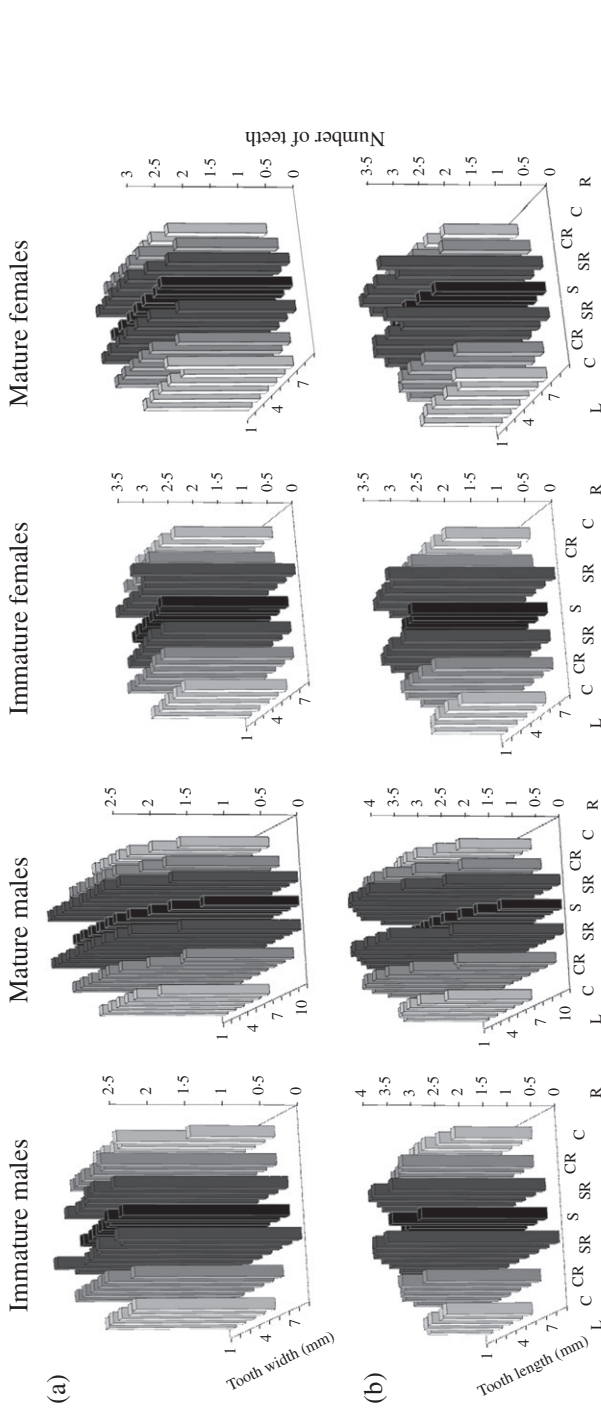
Fig. 5. Mean values of (a) width and (b) length of upper-jaw teeth from the left (L) and right (R) hemimandibles of *Amblyraja doellojuradoi*. S, symphysis row; SR, symphysis region row; CR, commissure region row; C, commissure row.
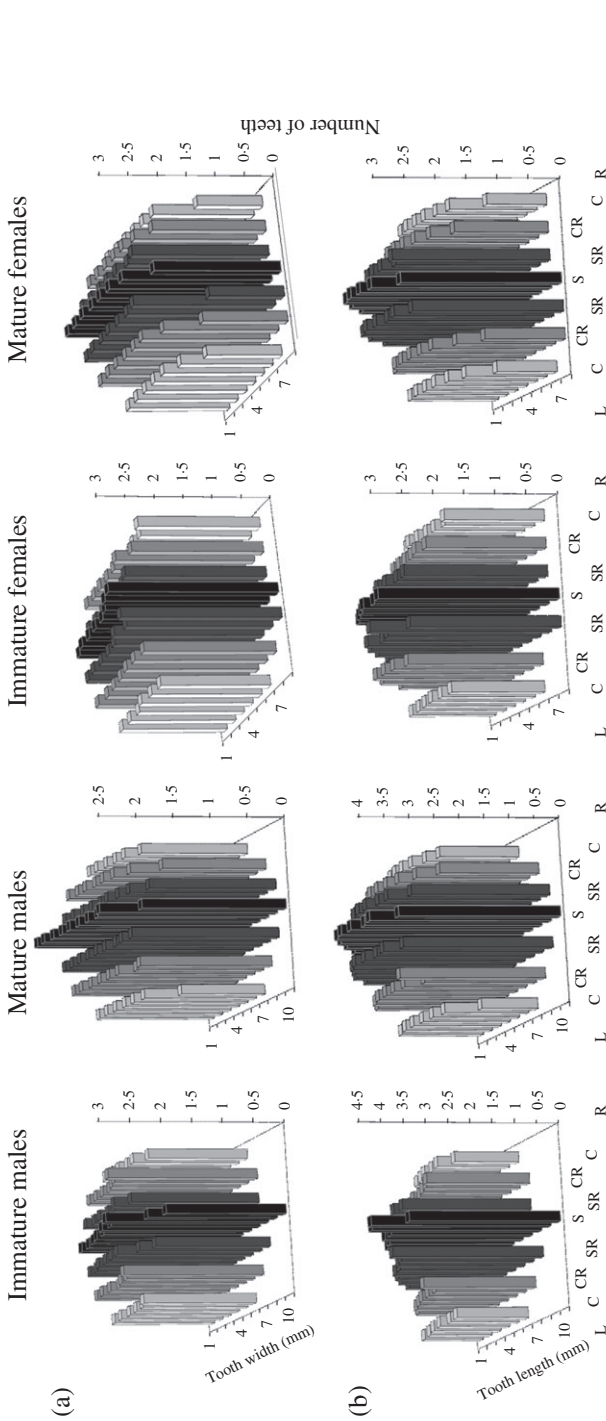
Fig. 6. Mean values of (a) width and (b) length of lower-jaw teeth from the left (L) and right (R) hemimandibles of *Amblyraja doellojuradoi*. S, ▪, symphysis row; SR, ▪, symphysis region row; CR, ▫, commissure region row; C, ▫, commissure row.

TABLE I. Results of the analysis of the mean length of each region of the upper and lower jaws of *Amblyraja doellojuradoi*. The number of teeth between which there were significant differences using Kruskal–Wallis test (P < 0.05) and Dunn's test (P < 0.05), are separated by dashes

	Upper jaw				Lower jaw			
	Comm	Comm.R	Sym.R	Sym	Comm	Comm.R	Sym.R	Sym
Mature males	* 1–2; 1–3	* 1–2; 1–3; 2–3	* 1–2; 1–3; 1–4; 1–5; 2–4; 2–5; 3–5	* 1–2; 1–3; 1–4; 2–3; 2–4	NS	* 1–3; 1–4; 1–5	* 1–2; 1–3; 1–4; 1–5; 2–4, 2–5; 3–5	* 1–2; 1–3; 1–4; 1–5; 1–6; 2–4; 2–5; 2–6; 3–5; 3–6
Immature males	NS	* 1–2; 1–3	* 1–3; 1–4; 2–4	* 1–3; 1–4	NS	* 1–4	* 1–3; 1–4	* 1–3; 1–4; 1–5; 2–5
Mature females	NS	* 1–2; 1–3; 1–4	* 1–2; 1–3; 1–4; 2–3; 2–4	* 1–2; 1–3; 2–4	NS	* 1–3; 1–4	* 1–2; 1–3; 1–4; 2–3; 2–4	* 1–2; 1–3; 1–4; 1–5; 2–3; 2–4; 2–5; 3–5
Immature females	* 1–3	* 1–2; 1–3; 1–4	* 1–2; 1–3	* 1–2; 1–3	NS	* 1–3; 1–4; 1–5	* 1–3; 1–4; 2–4	* 1–3; 1–4; 1–5; 2–4; 2–5

Comm, teeth from the commissure row; Comm.R, teeth from the commissure region; Sym.R, teeth from the symphysis region; Sym, teeth from the symphysis.
*P < 0.05.
NS, P > 0.05.

TABLE II. Best generalized linear models explaining the morphometric variation of the teeth of *Amblyraja doellojuradoi*. The intercept and coefficient are given for each of four dependent variables along with the AIC and Akaike's weights (w)

Intercept (±S.E.)	Coefficients (±S.E.)	AIC	w
Width of the teeth of the upper jaw			
2·4931 (±0·0162)	−0·1257 (±0·0142)Males + 0·1975 (±0·02)Comm.R −0·1257 (±0·0142)Males + 0·2886 (±0·02)Sym.R −0·1257 (±0·0142)Males + 0·1768 (±0·02)Sym	4462·9	0·728
Length of the teeth of the upper jaw			
2·2601 (±0·0244)	0·1794 (±0·0162)Males + 0·1283 (±0·0209)Mature + 0·3026 (±0·0227)Comm.R 0·1794 (±0·0162)Males + 0·1283 (±0·0209)Mature + 0·3835 (±0·0227)Sym.R 0·1794 (±0·0162)Males + 0·1283 (±0·0209)Mature + 0·2496 (±0·0227)Sym	4873·1	0·99
Width of the teeth of the lower jaw			
2·4032 (±0·0156)	−0·1358 (±0·0137)Males + 0·1961 (±0·0193)Comm.R −0·1358 (±0·0137)Males + 0·2738 (±0·0193)Sym.R −0·1358 (±0·0137)Males + 0·3967 (±0·0193)Sym	4326·2	0·731
Length of the teeth of the lower jaw			
2·1110 (±0·0245)	0·1583 (±0·0163)Males + 0·1307 (±0·021)Mature + 0·2613 (±0·0228)Comm.R 0·1583 (±0·0163)Males + 0·1307 (±0·021)Mature + 0·4778 (±0·0228)Sym.R 0·1583 (±0·0163)Males + 0·1307 (±0·021)Mature + 0·5317 (±0·0228)Sym	4742·3	0·99

Sym.R, teeth from the symphysis region; Sym, teeth from the symphysis.

DISCUSSION

An important characteristic of the dentition of chondrichthyans is that they are poliphiodonts, *i.e*. new teeth are replacing the worn or damaged during the course of the individual's life (Kemp, 1999). Most dental studies have focused mainly on brief and incomplete descriptions of the external and internal morphology of the teeth and are restricted to reports of the number of teeth, arrangement and absence or presence of dental sexual dimorphism (Feduccia & Slaughter, 1974; Du Buit, 1978; Sáez & Lamilla, 1997, 2004). A previous, qualitative analysis of the dentition of *A. doello-juradoi* showed that this species has a gradient monognathic heterodonty (Delpiani *et al.*, 2012), meaning that there is a gradual variation in the tooth morphology along the parallel axis of the jaw. *Amblyraja radiata* has the same sort of dentition, according to the description given by Herman *et al.* (1995).

There are few detailed morphometric works about rajid teeth. Some of them show that teeth of the first series (external) are shorter than the others, indicating a high wear (Rivera, 2009; Shimabukuro, 2009). In the present paper it was found that, based on the high degree of wear, the third teeth of each row corresponds to the series that participates in the bite (functional). Therefore, it is recommended not to use the teeth of the first two rows in morphometric studies, as they have a characteristic wear.

The counting of rows of teeth has been used to diagnose species of sharks, rays and skates. It is an easy character to assess, but can be unreliable (Bass, 1973). A problem may arise with growth of individuals, because the rows of teeth may shift as they increase in size (Bass, 1973). Sexual differences may also affect the number of teeth rows (Bass, 1973). For example, in the yellownose skate *Zearaja chilensis* (Guichenot 1848), females have more rows in the upper than in the lower jaw (Sáez & Lamilla, 1997). In the case of *A. doellojuradoi* the range in the number of rows of teeth (24–37 upper jaw; 24–35 lower jaw) are very different from those that have been observed in other species of this genus: *e.g. A. radiata* has 36–46 rows (Shark Trust, 2009); *A. frerichsi* has 36–42 rows in the upper and 37–40 in the lower jaw (Bustamante *et al.*, 2012); *A. jenseni* has 52–63 in the upper and 54–61 in the lower jaw (Orlov & Cotton, 2011). This marked difference in the number of tooth rows between *A. doellojuradoi* and other species of *Amblyraja* may be due to the maximum size of each species. *Amblyraja doellojuradoi* reaches *c.* 50–69% of the maximum L_T of the other species (*A. doellojuradoi* $L_{Tmax} = 59$ cm; *A. frerichsi* $L_{Tmax} = 120$ cm; *A. jenseni* $L_{Tmax} = 85$ cm; *A. radiata* $L_{Tmax} = 105$ cm).

The number of tooth rows of *A. doellojuradoi* remains constant throughout ontogeny and does not differ between sexes in both jaws. Both sexes, however, have a greater number of teeth in the upper than in the lower jaw. This pattern has been observed in other species such as the broadnose skate *Bathyraja brachyurops* (Fowler 1910) (Belleggia, 2007), the greytail skate *Bathyraja griseocauda* (Norman 1937) (Sáez & Lamilla, 2004) and the Magellan skate *Bathyraja magellanica* (Philippi 1902) (Rivera, 2009).

In the upper jaw, an increase in tooth width and length from the commissural to the symphysis region was found, whereas the symphysis teeth themselves present lower values than commissural ones. In the case of the lower jaw, an increase in width and length from the commissural teeth to the symphysis row was observed, showing the latter as having the highest values. According to Sáez & Lamilla (2004), the decreasing size of the teeth as they approach the commissure could facilitate the closure of the

jaws. The smaller size of the teeth in this area could also be related to its minor importance during prey grasping as compared with symphyseal teeth. In *A. doellojuradoi* the symphyseal teeth of the lower jaw would be more involved in this function.

Ontogenetic heterodonty occurs in *A. doellojuradoi* only in tooth length of males, with longer teeth in the mature ones. In females this heterodonty was not evident, since both width and length were constant in immature and mature specimens. The same pattern was found in the smallthorn sand skate *Psammobatis rudis* Günther 1870 and the shortfin sand skate *Psammobatis normani* McEachran 1983, both of which present ontogenetic heterodonty in males but not in females (Mabragaña & Giberto, 2007). The ontogenetic change in male dentition, from teeth with more rounded cusps to teeth with sharp conical cusps, is common in several species of skates (McEachran, 1977; Smale & Cowley, 1992; Braccini & Chiaramonte, 2002; Farias *et al.*, 2006; Treloar *et al.*, 2007). This is consistent with the results reported by Leible (1988) and Taniuchi & Shimizu (1993) who indicate that the tooth varies according to the size and the maturity of the specimen. Few authors postulate that dental changes associated with maturation are primarily due to better exploitation of the trophic niche, but in *A. doellojuradoi* this is not the case, since immature and mature feed almost on the same prey items (Delpiani *et al.*, 2013).

In addition, differences in tooth morphology between sexes were observed in *A. doellojuradoi*. In both jaws, males have longer cusps and narrower bases than females. The same heterodonty was found in the white-dotted skate *Bathyraja albomaculata* (Norman 1937) (Shimabukuro, 2009), *Bathyraja macloviana* (Norman 1937) (Rivera, 2009), *Z. chilensis* (Sáez & Lamilla, 1997) and other batoids (Bigelow & Schroeder, 1953). Sexual heterodonty has been interpreted in diverse ways by different authors. Feduccia & Slaughter (1974) suggested that the sexual dimorphism in dentition is associated with different dietary habits of males and females, reducing intraspecific competition. Kajiura & Tricas (1996) proposed that sexual heterodonty could increase feeding efficiency in both sexes and also in males increase reproductive success. This relationship between sexual dimorphism and reproduction was previously suggested by McEachran (1977) who also postulated that if the sexual heterodonty was due to a subdivision of the niche, then these differences would be manifest over a lifetime and not only in mature specimens. Therefore, these differences between sexes were associated with males using their jaws for restraining females during mating. In the case of *A. doellojuradoi* the most important difference in diet between sexes is the intake of fishes, being higher in females than in males (Delpiani *et al.*, 2013). This would be in conflict with the hypothesis of differential niche utilization by sexes given by Feduccia & Slaughter (1974), because if tooth morphological differences were due to different roles in prey capture, pointed teeth would be related to ichthyophagy, but males have such teeth, not females. Moreover, mature males have narrower teeth than females, having more space between rows, which could provide greater capacity to hold females firmly in apprehension during reproduction. Therefore, as previously noted by other authors for some species (Taniuchi & Shimizu, 1993; Tricas *et al.*, 1997), the dental dimorphism observed in *A. doellojuradoi* could be attributed to the use of the jaws of males to hold females during copulation.

References

Anderson, D. R., Burnham, K. P. & Thompson, W. I. (2000). Null hypothesis testing problems, prevalence and an alternative. *Journal of Wildlife Management* **64,** 912–923.

Applegate, S. P. (1965). Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. *Contribution in Science L.A. County Museum* **86,** 3–18.

Bass, A. J. (1973). Analysis and description of variation in the proportional dimensions of scyliorhinid, carcharhinid and sphyrnid sharks. *South African Association for Marine Biological Research* **32,** 1–27.

Becker, M. A., Chamberlain, J. A. & Stoffer, P. W. (2000). Pathologic tooth deformities in modern and fossil chondrichthyans: a consequence of feeding-related injury. *Lethaia* **33,** 103–118.

Belleggia, M. (2007). Ecología trófica de la raya de cola corta, *Bathyraja brachyurops* (Fowler, 1910), en el Atlántico sudoccidental. PhD Thesis, Universidad Nacional de Mar del Plata, Argentina.

Bigelow, H. B. & Schroeder, W. C. (1953). *Fishes of the Western North Atlantic. Part 2. Saw-fishes, Guitarfishes, Skates, Rays and Chimaeroids. Memoir of the Sears Foundation for Marine Research*. New Haven, CT: Yale University.

Braccini, J. M. & Chiaramonte, G. E. (2002). Intraspecific variation in the external morphology of the sand skate. *Journal of Fish Biology* **61,** 959–972.

Budker, P. (1971). *The Life of Sharks*. New York, NY: Columbia University Press.

Bustamante, C., Lamilla, J., Concha, F., Ebert, D. A. & Bennett, M. B. (2012). Morphological characters of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) (Rajiformes: Raji-dae), with notes on its biology. *PLoS One* **7,** 1–10.

Cailliet, G. M., Love, M. S. & Ebeling, A. W. (1986). *Fishes a Field and Laboratory Identifica-tion and Natural History*. Long Grove, IL: Waveland Pr Inc..

Crawley, M. J. (2005). *Statistics: An Introduction Using R*. Chichester: Wiley.

Delpiani, G. (2016). Reproductive biology of the southern thorny skate *Amblyraja doellojuradoi* (Chondrichthyes, Rajidae). *Journal of Fish Biology* **88,** 1413–1429.

Delpiani, G., Figueroa, D. E. & Mabragaña, E. (2012). Dental abnormalities of the southern thorny skate *Amblyraja doellojuradoi* (Chondrichthyes, Rajidae). *Revista de Biología Marina y Oceanografía* **47,** 135–140.

Delpiani, G., Spath, M. C. & Figueroa, D. E. (2013). Feeding ecology of the southern thorny skate, *Amblyraja doellojuradoi* (Pozzi, 1935) on the Argentine continental shelf. *Journal of the Marine Biological Association of the United Kingdom* **93,** 2207–2216.

Du Buit, M. H. (1978). Remarques sur la dentadure des raies et sur leur alimentation. *Vie et Milieu* **28,** 165–174.

Farias, I., Figueiredo, I., Serra-Pereira, B., Bordalo-Machado, P., Moura, T. & Serrano Gordo, L. (2006). Diet comparison of four ray species [*Raja clavata* Linnaeus 1758; *Raja brachyura* Lafont 1873; *Leucoraja naevus* (Müller & Henle 1841) and *Raja montagui* Fowler 1910] caught along the Portuguese continental coast. *Aquatic Living Resources* **19,** 105–114.

Feduccia, A. & Slaughter, B. H. (1974). Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution* **28,** 164–168.

Franklin, A. B., Shenk, T. M., Anderson, D. R. & Burnham, K. P. (2001). Statistical model selection: an alternative to null hypothesis testing. In *Modeling in Natural Resource Man-agement: Development, Interpretation and Application* (Shenk, T. M. & Franklin, A. M., eds), pp. 75–89. Washington, D.C.: Island Press.

Gutteridge, A. N. & Bennett, M. B. (2014). Functional implications of ontogenetically and sex-ually dimorphic dentition in the eastern shovelnose ray, *Aptychotrema rostrata*. *Journal of Experimental Biology* **217,** 192–200.

Herman, J., Hovestadt-Euler, M., Hovestadt, D. C. & Stehmann, M. (1994). Part B: Batomor-phii N° 1a: Order Rajiformes- Suborder Rajoidei- Family: Rajidae-Genera and subgen-era: *Anacanthobatis* (*Schroederobatis*), *Anacanthobatis* (*Springeria*), *Breviraja*, *Dacty-lobatus*, *Gurgesiella* (*Gurgesiella*), *Gurgesiella* (*Fenestraja*), *Malacoraja*, *Neoraja* and *Pavoraja*. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of chondrichthyan fishes. *Bulletin de L´Institut Royal des Sciences Naturelles de Belgique, Biologie* **64,** 165–207.

Herman, J., Hovestadt-Euler, M., Hovestadt, D. C. & Stehmann, M. (1995). Part B: Batomorphii N° 1b: Order Rajiformes- Suborder Rajoidei- Family: Rajidae-Genera and subgenera: *Bathyraja* (with a deep-water, shallow-water and transitional morphotype), *Psammo-batis*, *Raja* (*Amblyraja*), *Raja* (*Dipturus*), *Raja* (*Leucoraja*), *Raja* (*Raja*), *Raja* (*Rajella*) (with two morphotypes), *Raja* (*Rioraja*), *Raja* (*Rostroraja*), *Raja lintea* and *Symptery-gia*. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of condrichthyan fishes. *Bulletin de L´Institut Royal des Sciences Naturelles de Belgique, Biologie* **65,** 237–307.

Herman, J., Hovestadt-Euler, M., Hovestadt, D. C. & Stehmann, M. (1996). Part B: Batomor-phii N° 1c: Order Rajiformes- Suborder Rajoidei- Family: Rajidae-Genera and subgen-era: *Arhynchobatis*, *Bathyraja richardsoni*-type, *Cruriraja*, *Irolita*, *Notoraja*, *Pavoraja* (*Insentiraja*), *Pavoraja* (*Pavoraja*), *Pseudoraja*, *Raja* (*Atlantoraja*), *Raja* (*Okamejei*) and *Rhinoraja*. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of chondrichthyan fishes. *Bulletin de L´Institut Royal des Sciences Naturelles de Belgique, Biologie* **66,** 179–236.

Hubbs, C. L. & Ishiyama, R. (1968). Methods for the taxonomic study and description of the skates (Rajidae). *Copeia* **1968,** 483–491.

Johnson, J. B. & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19,** 101–108.

Kajiura, S. M. & Tricas, T. C. (1996). Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray, *Dasyatis sabina*. *Journal of Experimental Biology* **199,** 2297–2306.

Kemp, N. E. (1999). Integumentary system and teeth. In *Sharks, Skates and Rays. The Biology of Elasmobranchs Fishes* (Hamlett, W. C., ed), pp. 43–68. Baltimore, MD: Johns Hopkins University Press.

Lagler, K. F., Bardach, J. E., Miller, R. R. & May Passino, D. R. (1977). *Ichthyology*. New York, NY: John Wiley & Sons, Inc..

Leible, M. D. (1988). Revisión de métodos para estudios taxonómicos de rayas (Rajiformes: Rajidae). *Zoología* **52,** 15–93.

Lucifora, L. O., García, V. B., Menni, R. C., Escalante, A. H. & Hozbor, N. M. (2009). Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* **24,** 109–118.

Mabragaña, E. & Giberto, D. A. (2007). Feeding ecology and abundance of two sympatric skates, the shortfin sand skate *Psammobatis normani* (McEachran) and the smallthorn sand skate *P. rudis* (Günther) (Chondrichthyes, Rajidae), in the southwest Atlantic. *ICES Journal of Marine Science* **64,** 1017–1027.

McEachran, J. D. (1977). Reply to "sexual dimorphism in skates (Rajidae)". *Evolution* **31,** 218–220.

McEachran, J. D., Boesch, D. F. & Musick, J. A. (1976). Food division within two sympatric species-pairs of skates (Pisces, Rajidae). *Marine Biology* **35,** 301–317.

Miyake, T. & McEachran, J. D. (1988). Three new species of the stingray genus *Urotrygon* (Myliobatiformes: Urolophidae) from the eastern Pacific. *Bulletin of Marine Science* **42,** 366–375.

Moss, S. A. (1972). Tooth replacement and body growth rates in smooth dogfish, *Mustelus canis* (Mitchill). *Copeia* **1972,** 808–811.

Orlov, A. M. & Cotton, C. F. (2011). Sexually dimorphic morphological characters in five North Atlantic deepwater skates (Chondrichthyes: Rajiformes). *Journal of Marine Biology* **2011,** 18 pp. http://dx.doi.org/10.1155/2011/842821.

Pratt, H. L. & Carrier, J. C. (2001). A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes* **60,** 157–188.

Rivera, P. (2009). Dentición de *Bathyraja macloviana* (Norman, 1937) y *Bathyraja magellanica* (Philippi, 1902) (Chondrichthyes, Familia Rajidae). PhD Thesis, Universidad Nacional de Mar del Plata, Argentina.

Sáez, S. & Lamilla, J. (1997). Morfología y disposición dentaria en una especie con heterodontía sexual: *Raja* (*Dipturus*) *chilensis* Guichenot, 1848. *Biología Pesquera* **26,** 25–41.

Sáez, S. & Lamilla, J. (2004). Sexual homodonty in *Bathyraja griseocauda* (Norman, 1937) from the southern eastern Pacific (Chile) (Chondrichthyes, Rajidae: Arhynchobatinae). *Journal of Applied Ichthyology* **20,** 189–193.

Shimabukuro, V. (2009). Hábitos alimentarios y dentición de *Bathyraja albomaculata* (Norman, 1937) (Chondrichthyes: Rajidae). PhD Thesis, Universidad Nacional de Mar del Plata, Argentina.

Smale, M. J. & Cowley, P. D. (1992). The feeding ecology of skates (Batoidea: Rajidae) off the Cape south coast, South Africa. *South African Journal of Marine Science* **12,** 823–834.

Stehmann, M. F. W. (2002). Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Archive of Fishery and Marine Research* **50,** 23–48.

Taniuchi, T. & Shimizu, M. (1993). Dental sexual dimorphism and food habits in the stingray *Dasyatis akajei* from Tokyo Bay, Japan. *Nippon Suisan Gakkaishi* **59,** 53–60.

Treloar, M. A., Laurenson, L. J. B. & Stevens, J. D. (2007). Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters. *Environmental Biology of Fishes* **80,** 181–196.

Tricas, T. C., Deacon, K., Last, P., McCosker, J., Walker, T. & Taylor, L. (1997). *Sharks and Rays*. London: Harper Collins Publishers.

Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S-Plus*. New York, NY: Springer.

Zuur, A. F., Ieno, E. N. & Meesters, E. (2009). *A Beginner's Guide to R*. New York, NY: Springer.

Electronic Reference

Shark Trust (2009). An Illustrated Compendium of Sharks, Skates, Rays and Chimaera, *Amblyraja radiata. ID Guide*. Available at http://www.sharktrust.org/shared/downloads/id_guides/starry_skate_st_id_guide.pdf/ (last accessed 27 April 2016).