The dentition of the narrownose smooth-hound shark, *Mustelus schmitti*

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Abstract. The present study provides a quantitative and qualitative analysis on the dentition of *Mustelus schmitti*, and estimates the tooth-replacement rate. In total, 47 males and 56 females of *M. schmitti* were collected on scientific trawl surveys conducted by the National Institute of Fisheries Research and Development (INIDEP) in Argentina during the months of November 2007, November 2008 and December 2008. The dental laminas were extracted from the jaw cartilage and attached to onionskin paper for dehydration treatment, maintaining the original jaw position. Tooth replacement rate was estimated following established methods used for fossil sharks, instead of the established technique of clipping teeth, based on the premise that tooth length within each row decreases from the lingual to the labial side of the jaw as a consequence of wear. The length difference between consecutive teeth in four representative rows should be proportional to the tooth-replacement rate. *Mustelus schmitti* exhibited homodont dentition, where teeth were similar in shape or design, and are arranged in a semi-pavement-like dentition. The dental formula was 47-63/50-63 for juveniles and 50-77/50-69 for adult specimens. The estimated mean replacement rate was 4 days series^{-1}.

Introduction

The teeth of chondrichthyans are polyphyodont, which means that they are continuously replaced (Motta 2004; Cousseau 2010). The newly formed teeth move forward, as in a conveyor belt, organised in rows and series on the palatoquadrate and Meckel's cartilage (Motta 2004). A row is a single line of teeth transverse to the longitudinal jaw axis that includes both functional teeth and their replacements. Series is used for a line of teeth along the jaws that is parallel to the jaw axis and includes teeth from all rows (Compagno 2003; Motta 2004). The replacement rates in sharks vary from 2 to 70 days series^{-1}, and are affected by age of the animal, diet, season and water temperature (Reif *et al.* 1978; Luer *et al.* 1990; Overstrom 1991). The evolutionary reason for this process may be to maintain sharpness and cutting ability, and, as in other poikilotherms with indeterminate growth, allow the replacement of smaller teeth by larger ones because such teeth cannot grow once they have erupted (Moss 1972; Motta 1984; Whitenack *et al.* 2011). Most studies have investigated replacement rates on extant sharks by clipping teeth (Reif *et al.* 1978; Luer *et al.* 1990; Overstrom 1991), whereas studies of fossil sharks have used another method based on the reduction in tooth length within each row,

from the lingual to the labial side of the jaw as a consequence of wear (Botella *et al.* 2009).

Diverse branches of ichthyology use teeth as their object of study. The cartilaginous skeletons of chondrichthyans are not easily fossilised, so teeth are more often found than skeletons in the fossil record (Compagno 2003). The importance that teeth have as a means of distinguishing and classifying elasmobranchs has long been known to phylogenists, paleontologists, comparative anatomists and taxonomists (Long 1994; Purdy and Francis 2007; Adnet and Cappetta 2008; Straube *et al.* 2008; Maisey 2012). There are multiple shark descriptions concerning the systematic significance of tooth morphology (Bigelow and Schroeder 1953; Compagno 1984*a*, 1984*b*, 2001; Duhamel and Compagno 1988; Grace 2001; Meneses and Paesch 2003; Lamilla and Bustamante 2005; Figueroa 2011), and even taxonomic dental keys that allow diagnoses of different shark species (Sáez and Pequeño 2010). There have been more studies on the dentition on batoids than sharks (Herman *et al.* 1994, 1995, 1996; Kajiura and Tricas 1996; Sáez and Lamilla 1997, 2004, 2012; Braccini and Chiaramonte 2002; Rivera 2009; Shimabukuro 2009; Delpiani *et al.* 2012). However, there have been excellent studies on the dentition of a few species in
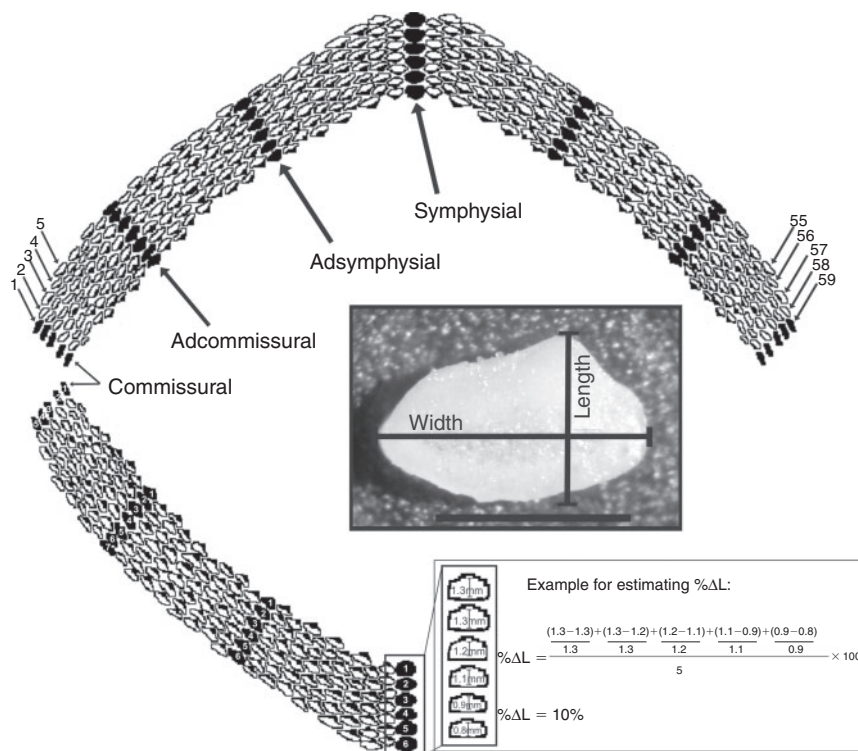
Fig. 1. Diagram illustrating upper and lower jaw of *Mustelus schmitti*, and the technical method of count rows. The image shows measurements (width and length) taken from all the teeth located on the symphysial, adsymphysial, adcommissural and commissural rows. An illustrative example for estimating size increment in length (%ΔL) is presented inside the box in the lower-right corner of the figure.

Argentina, including the narrowmouthed catshark, *Schroederichthys bivius* (Gosztonyi 1973), and the sand tiger shark, *Carcharias taurus* (Lucifora *et al.* 2001, 2003).

The genus *Mustelus* is the most speciose genus of Triakidae, comprising at least 31 species (Nelson 2006; Heemstra 1997; Pérez Jiménez *et al.* 2005; White and Last 2006, White and Last 2008; Cubelio *et al.* 2011). The narrownose smooth-hound shark, *Mustelus schmitti*, inhabits coastal waters from southern Florianópolis (27°S, Brazil) to Ría Deseado (47°45′S, Argentina). It is found from the shallow waters down to 120-m depth (Cousseau and Perrotta 2004). In Brazil, the depth range extends down to 195 m (Heemstra 1997). Its diet consists mostly of crabs (Capitoli *et al.* 1995; Chiaramonte and Pettovello 2000; Molina and López Cazorla 2011), but polychaetes and fish could be the most important prey in some regions as the total length of the predator shifts (Belleggia *et al.* 2012). The specific goals of the present paper are (1) to provide a quantitative and qualitative analysis on the dentition of *M. schmitti* and (2) to estimate the tooth-replacement rate.

Materials and methods

In total, 103 specimens of *M. schmitti* (47 males and 56 females) were collected on scientific trawl surveys conducted by The National Institute of Fisheries Research and Development (INIDEP) in Argentina, during the months of November 2007, November 2008 and December 2008. Specimens were measured (total length (TL), mm) and sexed. Maturity stage (juveniles or adults) was determined according to the degree of clasper calcification, development of testes and reproductive ducts in males, and on the condition of uteri, oviducal glands and ovarian follicles in females (Stehmann 2002). The jaws were excised, frozen and returned to the laboratory for subsequent analysis. Once in the laboratory, dental laminas were extracted from the jaw cartilage and attached to onionskin paper for dehydration treatment, maintaining their original jaw position.

Quantitative analyses

Mustelus species have teeth arranged in rows on the palatoquadrate and Meckel cartilages (Motta 2004), forming a semipavement dentition for crushing prey (Compagno 2003). The total number of tooth rows in each jaw was recorded (Fig. 1). A useful tool in systematics is the dental formula, which is the total number of rows in each jaw (maximum and minimum scores in upper jaw/maximum and minimum scores in lower jaw). The number of rows was analysed with Mann–Whitney *U* test to search significant differences between upper and lower jaws. Moreover, the relationship between tooth rows and TL of *M. schmitti* was evaluated by fitting quantile regression models (Koenker and Bassett 1978; Cade and Noon 2003) at 50% (simple linear regression model), 90% and 10% levels (most extreme values in the dataset) with the *quantreg* R 2.15.3 package (Koenker 2007; R Core Development Team 2013).

The tooth measurements were carried out on four representative rows in each jaw, over the dental laminas previously attached to onionskin paper (Fig. 1). The selected rows were

defined as (Rivera 2009) (1) symphysial (row located at the symphysis in the middle of the jaw), (2) adsymphysial (row located at 10 rows from the symphysis), (3) adcommissural (row located at 10 rows from the commissure) and (4) commissural (row located at the commissure where two jaws are joined) (Fig. 1). The tooth located closest to the lingual side of the mouth was named Tooth 1, and a correlative numeration (e.g. 2, 3) was maintained up to the oldest labial tooth (Fig. 1). The width and length of each tooth were measured in the four representative rows in both lower and upper jaws, as in Sáez and Lamilla (1997; Fig. 1). The tooth measurements were carried out using a magnifying glass equipped with an ocular micrometer to the nearest 0.01 mm. The mean length and width of the teeth were compared among jaws, rows and groups by using a paired Student's *t*-test, to fully assess the significance of results.

Replacement rate

The tooth-replacement rate was estimated following the technique established for fossil sharks (Botella *et al.* 2009), instead of the established technique of clipping teeth, because *M. schmitti* is hard to maintain in captivity. In aquariums, this species exhibits erratic swimming behaviour and exhaustion, it may be preyed or harassed by other species, and ultimately death can result (J. Jañez, Temaiken Aquarium, pers. comm.). Thus, the method used on fossil sharks (Botella *et al.* 2009) was proposed for this species, and also for those species that are not adapted to captivity (Dehart 2004), as an alternative approach to the usual observations in living animals. The method is based on the differences that exist between wear of the functional teeth and wear of most recently formed teeth. The tooth length within each row decreases from lingual to labial as a consequence of wear. The length difference between consecutive teeth in each four representative rows measured in *M. schmitti* should be proportional to the tooth-replacement rate (Botella *et al.* 2009). On the basis of this, the size difference in length (%ΔL) in consecutive teeth in each selected row was estimated as

$$\%\Delta L = \frac{\sum \left(\text{Length tooth}_{ij} - \text{Length tooth}_{i(j+1)} \right) / \text{Length tooth}_{ij}}{N \text{ obs}},$$

where *i* is the row and *j* is the tooth position number. Moreover, Botella *et al.* (2009) pointed out that size difference averages of consecutive teeth plotted against mean tooth-replacement rates (days series^{-1}) for six different shark species exhibited a linear relationship, with a high correlation coefficient ($r^2 = 0.83$; Fig. 2, redrawn considering only extant sharks). The %ΔL for these six species was obtained by Botella *et al.* (2009) by measuring teeth, and plotted against their known replacement rates available in the literature, which are based on tooth clipping (Fig. 2). The %ΔL scores found in *M. schmitti* were extrapolated in the regression line (Fig. 2), making the leap from changes in tooth length to the replacement rates in days. In this way, this regression analysis developed for fossil sharks was applied to current sharks, instead of using the standard methodology of clipping teeth to establish tooth-replacement rate. To show variability surrounding %ΔL and replacement rates in days, 95% confidence intervals of each mean were constructed by resampling the observations 999 times. Bootstrap routine was
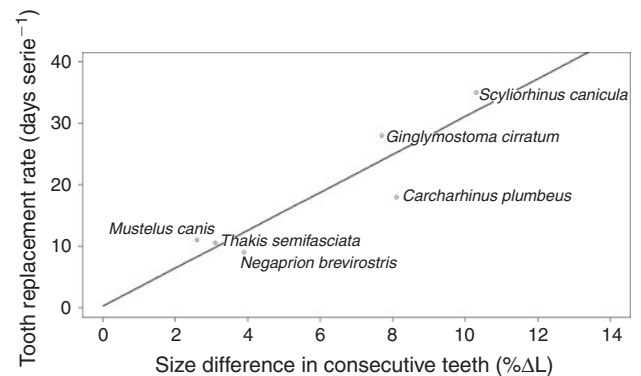

Fig. 2. Least-squares regression of tooth-replacement rates (days series^{-1}) against size difference in length in consecutive teeth (%ΔL). Figure was redrawn and adapted from Botella *et al.* (2009), considering only extant sharks.

carried out using R 2.15.3 and library *boot* (R Core Development Team 2013). Differences in the mean tooth-replacement rate among maturity stages and jaws were determined using Student's *t*-test.

Qualitative analyses

Accurate tooth observations of their morphology are hampered by poor visibility of attached teeth. Hence, teeth were removed from the onionskin paper, then cleaned by immersing them in a 5% aqueous potassium hydroxide (KOH) solution, and heated for 1 h. The isolated and cleaned teeth, and dental lamina, were mounted onto 15-cm aluminium plug. They were gold-coated in a Denton Vacuum Desk II gold-cathode sputter (Denton Vacuum LLC, Moorestown, NJ, USA) and analysed using a JSM-6460LV (Jeol, Tokyo, Japan) scanning electron microscope (SEM) operating at 15 kV accelerating voltage. Digital photographs were captured. A preliminary analysis indicated that there were no differences in tooth shape among both sexes and maturity stages. Therefore, qualitative information could be polled. The tooth terminology used throughout the paper is that proposed by Compagno (2003).

Results

Quantitative analyses

The lower jaw of *M. schmitti* showed two more tooth rows than did the upper jaw (Mann–Whitney $U = 4011$, $P = 0.002$; Table 1). The total number of rows varied between upper and lower jaws in both adult males and females (Mann–Whitney: males, $U = 534$, $P = 0.04$; females, $U = 1144.5$, $P = 0.005$). However, no significant differences were found between upper and lower jaws from juveniles specimens (Mann–Whitney: males, $U = 187.5$, $P = 0.43$; females, $U = 116$, $P = 0.90$; Table 1). The tooth-row counts did not present differences between sexes in either upper (Mann–Whitney: $U = 1377.5$, $P = 0.68$) or lower (Mann–Whitney: $U = 1494.5$, $P = 0.23$) jaw (Table 1). The dental formula of *M. schmitti* was 47-63/50-63 for juveniles, and 50-77/50-69 for adult specimens.

The total number of rows in *M. schmitti* increased with growth at minimum, medium and maximum values of row

counts, in either upper (10% quantile regression slope: 0.011, $P = 0.03$; 50% quantile regression slope: 0.01, $P = 0.025$; 90% quantile regression slope: 0.02, $P < 0.001$) and lower (10% quantile regression slope: 0.015, $P = 0.02$; 50% quantile regression slope: 0.014, $P < 0.001$; 95% quantile regression slope: 0.021, $P < 0.001$) jaws (Fig. 3).

The mean tooth length of all of the teeth from labial to lingual, in both jaws, decreased from symphysial to commissural row (Fig. 4*a*). The widest teeth were the adsymphysial, following by symphysial, adcommissural and commissural, respectively (Student's *t*-test, $P < 0.001$ for each case; Fig. 4*b*). Upper jaw showed longer teeth than did the lower one (Student's *t*-test: d.f. $= 5833$, $t = 4.68$, $P < 0.001$; Fig. 5*a*), whereas the lower jaw presented wider teeth than did the upper one (Student's *t*-test: d.f. $= 5806$, $t = 5.09$, $P < 0.001$; Fig. 5*b*).

Replacement rate

The size increment in length in consecutive teeth (%ΔL) ranged between 0.13 and 2.28, depending on row, sex and maturity stage (Table 2). The mean extrapolated value of tooth-replacement rate obtained for *M. schmitti* was 4 days series^{-1} (Table 3). The replacement rate ranged between 2 and 3 days series^{-1} in commissural tooth and between 4 and 5 days series^{-1} in symphysial, adcommissural and commissural tooth (Table 3). Finally, *M. schmitti* juveniles replaced their teeth at a slower rate (mean ± s.d., 4.523 ± 0.03 days series^{-1}) than did adults (3.982 ± 0.02 days series^{-1}) and this difference was significant (Student's *t*-test: d.f. $= 30290$, $t = 28.45$, $P < 0.001$). The upper jaw exhibited a replacement rate of 3.87 ± 0.02 days series^{-1}, whereas lower jaw replaced teeth at 4.64 ± 0.03 days series^{-1} (Student's *t*-test: d.f. $= 30779$, $t = 41.56$, $P < 0.001$; Table 3).

Qualitative analyses

Mustelus schmitti possesses a semi-pavement-like dentition (Fig. 6*a*). Teeth are similar is shape throughout its jaws, confirming the presence of homodont dentition. Teeth are divided into the crown, entirely covered by shiny enameloid, and the root that consists of porous dentine (Fig. 6*b*). The crown is short, and the cusp is reduced only to a low point. A peg, an elongated protuberance, extends from the lingual face of the crown just above the root (Fig. 6*c*). The transverse groove divides the root
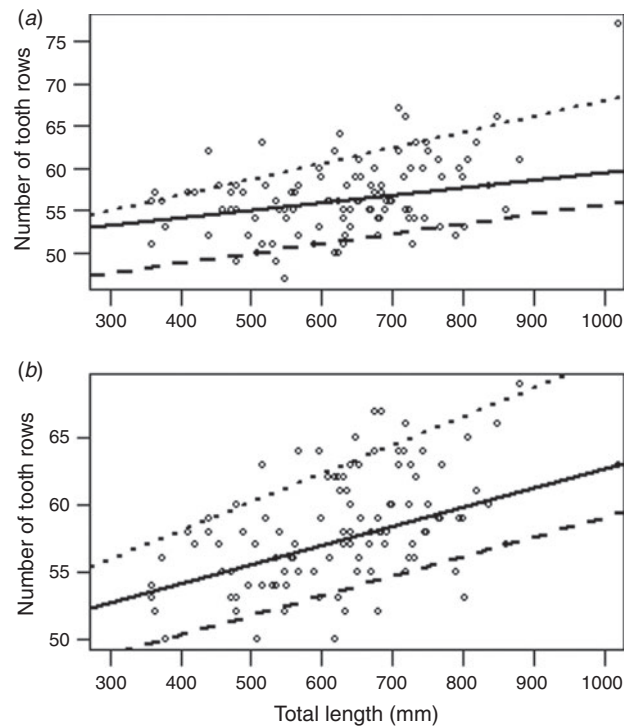

Fig. 3. Quantile regressions of tooth-row counts and total length of *Mustelus schmitti* in (*a*) upper jaw and (*b*) lower jaw. Dotted, solid, and dashed lines are 90%, 50%, and 10% quantile regressions, respectively.
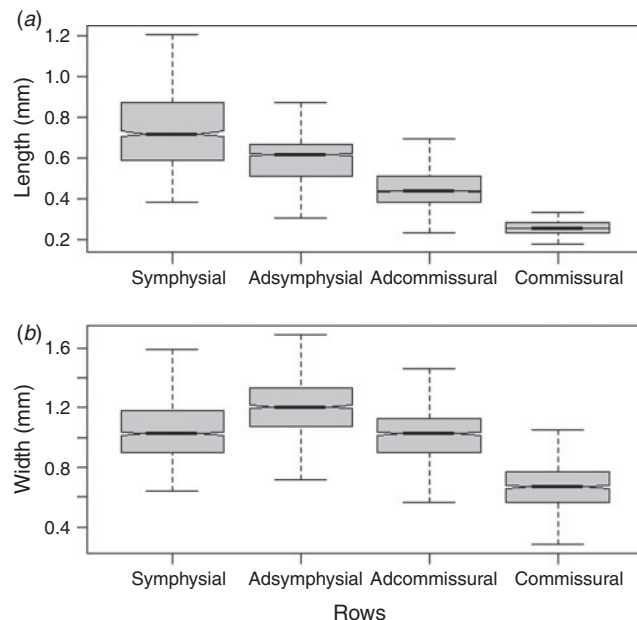

Fig. 4. Boxplot of (*a*) length and (*b*) width for all teeth from labial to lingual in both jaws, in symphysial, adsymphysial, adcommissural and commissural rows, from *Mustelus schmitti*. The notches are drawn in each side of the boxes, giving strong evidence for the statistical difference among medians in each row, because they do not overlap.

Table 1. Total number of specimens sampled (*n*), total length range (TL), and range, mean and s.d. of tooth-row counts in both upper and lower jaws in *Mustelus schmitti* by sex and maturity stage

Group	*n*	TL range (mm)	Number of tooth rows					
			Upper jaw			Lower jaw		
			Range	Mean	s.d.	Range	Mean	s.d.
Female								
Juvenile	15	360–568	47–63	55.13	3.68	52–63	55.67	2.94
Adult	41	612–1020	50–77	57.49	5.12	52–67	59.78	3.94
Male								
Juvenile	18	359–560	49–62	54.28	3.51	50–60	55.11	2.86
Adult	29	562–881	50–63	57.24	3.85	52–69	59.21	4.22

into mesial and distal lobes (Fig. 6*b*, *c*). It may extend over the extreme rim of the root to form a transverse notch (Fig. 6*b*). The central foramen communicates with the pulp cavity at the mid-length of the groove (Fig. 6*d*).

Discussion

Mustelus schmitti exhibits homodont dentition, where teeth are similar in shape or design, and arranged in a semi-pavement-like
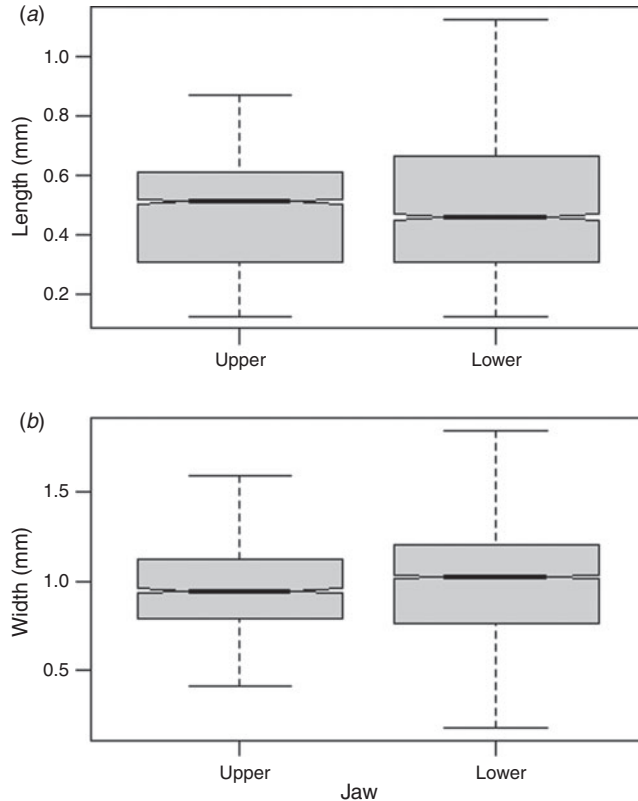

Fig. 5. Boxplot of (*a*) length and (*b*) width for all teeth in all of the rows measured, in upper and lower jaws, from *Mustelus schmitti*. The notches are drawn in each side of the boxes, giving strong evidence of the statistical difference among medians from each jaw, because they do not overlap.

dentition. The peg of each tooth extends under the basal ledge of the next tooth in succession in the same row. This arrangement, observed in many species of *Mustelus* and three species of *Triakis* (particularly *T. acutipinna*), probably serves to interlock the close-set teeth of the semi-pavement-like dentition (Compagno 2003). The transverse groove of the root that divides the attachment surface into mesial and distal lobes is common also in Rajidae (Herman *et al.* 1994, 1995, 1996; Sáez and Lamilla 1997, 2004; Rivera 2009; Shimabukuro 2009). These considerations about the morphology of the crown and root have significance for phylogenists, paleontologists, comparative anatomists and taxonomists, so as to accurately identify species on the basis of teeth (Long 1994; Purdy and Francis 2007). For instance, the teeth of *M. schmitti* are morphologically very similar to those of *M. vanderhoefti*, known until the Eocene (Adnet and Cappetta 2008).

The dental formula of *M. schmitti* was 47-63/50-63 for juvenile and 50-77/50-69 for adult specimens. These results are consistent with the average of the total number of tooth rows for Triakidae (Compagno 2003). However, dental formula alone is not useful for distinguishing the *Mustelus* species because of high intraspecific variation (Rosa and Gadig 2010). Moreover, tooth-row counts increased with total length of *M. schmitti*, especially in the lower jaw, where adult specimens showed two more tooth rows than in the lower one. In *M. henlei*, and probably some other species with small and numerous teeth, rows also increase in number with growth (Compagno 2003).

The reduction observed in tooth length from symphysis to commissure in *M. schmitti* is common and should not be termed monognathic heterodonty (Motta and Wilga 2001). Gradient monognathic heterodonty, where teeth exhibit a gradual variation in size along series, is a general phenomenon in the dentitions of sharks (Compagno 2003). Rajidae also showed gradient monognathic heterodonty, and this has been proposed as a feature to improve the ability of the jaws to close on the prey (Sáez and Lamilla 1997, 2004; Rivera 2009). Moreover, commissural teeth are smaller because of a less important role in grasping prey than for the symphysial teeth (Rivera 2009).

Mustelus schmitti, as do many shark species from the Carcharhiniformes, exhibits sexual homodonty (Compagno 2003). Dental sexual dimorphism is widespread in batoids (Bigelow and Schroeder 1953; Herman *et al.* 1995; Sáez and

Table 2. Means size increment in length (%ΔL) for consecutive teeth in commissural, adcommissural, adsymphysial and symphysial rows in *Mustelus schmitti*, by sex and maturity stage

The slash (/) separates the upper and lower jaw. The 95% bootstrap confidence intervals for the mean %ΔL are presented in parentheses

Sex and maturity stage	Commissural	Adcommissural	Adsymphysial	Symphysial	Average
Juvenile male	1.04 (1.02–1.05)/	1.74 (1.72–1.75)/	1.30 (1.28–1.31)/	1.64 (1.63–1.65)/	1.42 (1.41–1.43)/
	1.43 (1.40–1.46)	1.47 (1.45–1.49)	1.09 (1.06–1.12)	1.77 (1.75–1.79)	1.44 (1.43–1.46)
Juvenile female	0.43 (0.41–0.45)/	1.56 (1.54–1.59)/	1.46 (1.44–1.48)/	1.80 (1.78–1.82)/	1.31 (1.30–1.33)/
	0.71 (0.69–0.74)	1.61 (1.60–1.63)	2.14 (2.13–2.16)	2.11 (2.09–2.14)	1.65 (1.63–1.67)
Adult male	0.13 (0.11–0.14)/	1.37 (1.36–1.38)/	1.23 (1.21–1.24)/	1.27 (1.25–1.28)/	1.11 (1.09–1.13)/
	0.93 (0.92–0.95)	1.61 (1.59–1.63)	1.20 (1.19–1.22)	1.05 (1.03–1.06)	1.32 (1.31–1.33)
Adult female	0.65 (0.64–0.66)/	1.39 (1.38–1.40)/	1.25 (1.23–1.28)/	1.71 (1.69–1.73)/	1.14 (1.12–1.15)/
	1.33 (1.31–1.35)	1.56 (1.55–1.57)	2.28 (2.26–2.30)	1.50 (1.49–1.51)	1.56 (1.54–1.58)
Average	0.57 (0.56–0.58)/	1.50 (1.49–1.51)/	1.31 (1.30–1.32)/	1.60 (1.59–1.61)/	1.35 (1.34–1.36)/
	1.11 (1.10–1.13)	1.57 (1.56–1.58)	1.70 (1.68–1.72)	1.60 (1.58–1.61)	1.50 (1.49–1.51)

Table 3. Mean tooth-replacement rates (days series^{-1}) in bold type, obtained by extrapolating %ΔL values (Table 2) on the Fig. 2, for commissural, adcommissural, adsymphysial and symphysial rows, by sex and maturity stage

The slash (/) separates the upper and lower jaw. The 95% bootstrap confidence intervals for the mean tooth-replacement rate (days series^{-1}) are presented in parentheses

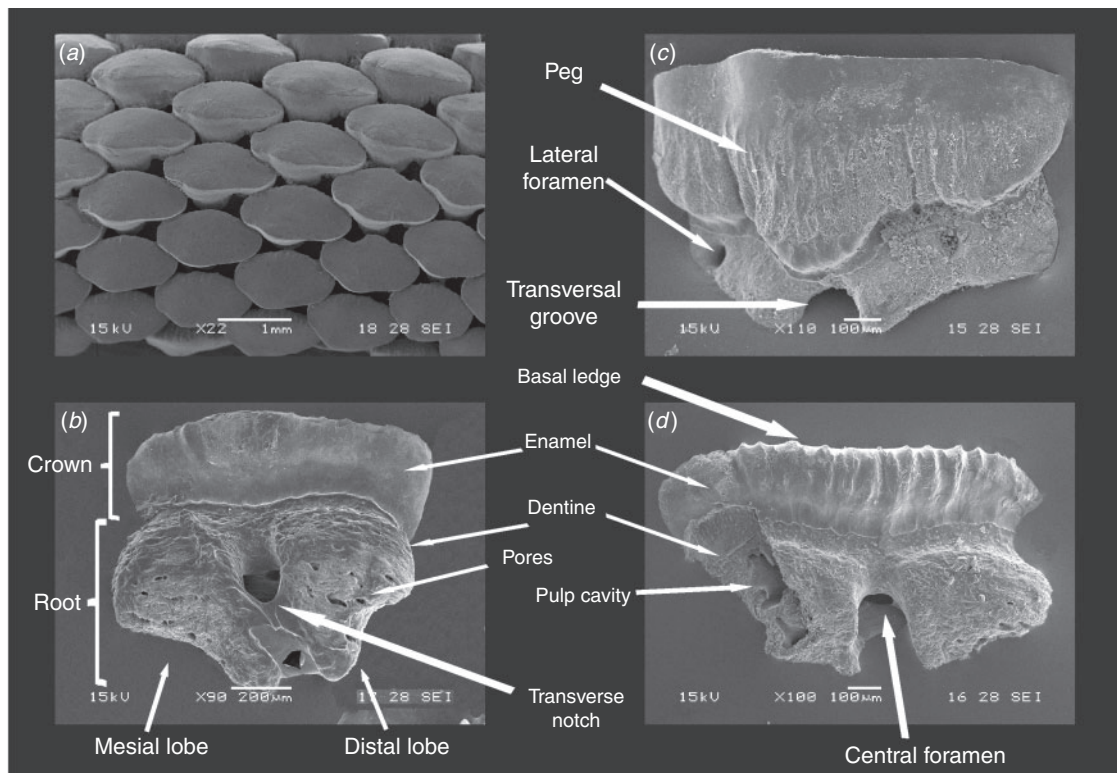| Sex and maturity stage	Commissural	Adcommissural	Adsymphysial	Symphysial	Average
Juvenile male	**3** (3–3)/**4** (4–5)	5 (5–5)/5 (4–5)	**4** (4–4)/**3** (3–3)	5 (5–5)/5 (5–6)	**4** (4–4)/**4** (4–5)
Juvenile female	**1** (1–1)/**2** (2–2)	**4** (4–4)/5 (5–5)	**4** (4–4)/**7** (6–7)	5 (5–5)/6 (6–7)	**4** (4–4)/5 (5–5)
Adult male	**1** (1–1)/**3** (3–3)	**4** (4–4)/5 (5–5)	**4** (4–4)/**4** (4–4)	**4** (4–4)/**3** (3–3)	**3** (3–4)/**4** (4–4)
Adult female	**2** (2–2)/**4** (4–4)	**4** (4–4)/5 (5–5)	**4** (4–4)/**7** (7–7)	5 (5–5)/5 (5–5)	**4** (3–4)/5 (5–5)
Average	**2** (2–2)/**3** (3–4)	5 (5–5)/5 (5–5)	**4** (4–4)/5 (5–5)	5 (5–5)/5 (5–5)	**4** (4–4)/5 (5–5)

Fig. 6. Scanning electron microscope images of the (*a*) dental lamina, (*b*) isolated teeth in labial view, (*c*) isolated teeth in lingual view and (*d*) isolated teeth in labial view exhibiting the pulp cavity, from *Mustelus schmitti.*

Lamilla 1997; Braccini and Chiaramonte 2002; Scenna *et al.* 2006) and has been primarily attributed to differential foraging by the sexes, so as to alleviate intraspecific competition for food (Feduccia and Slaughter 1974). However, tooth modifications in adult males may increase the grasping ability of the mouths during courtship (McEachran 1977; Kajiura *et al.* 2000). Sexual dimorphism in sharks from the south-western Atlantic Ocean has been demonstrated only in *Schroederichthys bivius* (Gosztonyi 1973), a species that does not show differences in diet between sexes (Sánchez *et al.* 2009), which probably indicates a positive correlation with reproductive patterns.

The decrease in tooth length within each row from the lingual to the labial side of the jaw, as a consequence of wear, allowed an estimation of the replacement rate in *M. schmitti*. This method, which is used on fossil sharks (Botella *et al.* 2009), did not aim to replace the standard methodology of clipping teeth; instead, it required the results from the classical approach. The method allowed to make a leap from tooth measures to replacement rates in days, and was proposed for species not adapted to captivity. For that purpose, more studies applying the standard technique of clipping teeth are needed, so as to find the best-fit line for the regression relationship between variables, and to assess with more accuracy the replacement rate in days.

The dentition pattern observed in *M. schmitti* and their fast replacement rate are characteristics of durophagous species that feed on crustaceans (Nikolsky 1963; Figueroa *et al.* 2009). Moreover, the replacement rate appeared also to be associated with tooth length. For instance, juvenile specimens had smaller teeth than did adults and showed slower replacement rates. Similarly, upper jaw exhibited longer teeth than did the lower

one, and a faster replacement rate. The estimated mean replacement rate was 4 days series^{-1}. Considering dental formulae and the replacement rate, *M. schmitti* replaces ∼5350 teeth each year throughout its lifetime. Previous research has shown that replacement rate varies from 10 to 12 days series^{-1} for *Mustelus canis* (Ifft and Zinn 1948), 9 to 12 days series^{-1} for *Triakis semifasciata* (Reif *et al.* 1978) and is 2 days series^{-1} for *Carcharias taurus* (Overstrom 1991). The replacement rate is species-specific and is affected by the age of the animal, diet, season and water temperature (Reif *et al.* 1978). For instance, winter water temperatures result in slower replacement rates in *Ginglymostoma cirratum* (Luer *et al.* 1990). The samples collected for the present work were obtained during the warm season (October–November). Thus, the replacement rate for *M. schmitti* may be longer during the cold season. However, additional sampling during the cold season is required to confirm this hypothesis.

Acknowledgements

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