SEASONAL DYNAMICS OF DENTAL SEXUAL DIMORPHISM IN THE ATLANTIC STINGRAY *DASYATIS SABINA*

STEPHEN M. KAJIURA* AND TIMOTHY C. TRICAS

Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, FL 32901-6988, USA

Summary

Cartilaginous fishes continuously replace their teeth throughout their life (polyphyodonty) and often show a sexually dimorphic dentition that was previously thought to be an invariant sex character. Radial vector analysis of tooth shape in the polyphyodontic stingray *Dasyatis sabina* across a consecutive 24 month period shows a stable molariform morphology for females but a periodic shift in male dentition from a female-like molariform to a recurved cuspidate form during the reproductive season. The grip tenacity of the male dentition is greater for the cuspidate form that occurs during the mating season than for the molariform dentition that occurs during the non-mating season. Dental sexual dimorphism and its sex-dependent temporal plasticity probably evolved *via* polyphyodontic preadaptation under selective pressures on both sexes for increased feeding efficiency and sexual selection in males to maximize mating success. These phenomena are important considerations for the identification and classification of cartilaginous fishes and possibly other polyphyodontic vertebrates in the fossil record.

Key words: elasmobranch, dentition, sexual dimorphism, stingray, *Dasyatis sabina*, Dasyatidae, phenotypic plasticity, seasonal, tooth morphology.

Introduction

The evolution of piscine dentition is thought to be driven by selective pressures that maximize feeding efficiency. The functional significance of the dentition in elasmobranchs differs from that of other fishes because it is used not only for feeding but also for male grasping of females during courtship and mating. Biting functions as a pre-copulatory releasing mechanism to invoke female cooperation during courtship, to facilitate insertion of the clasper and to maintain intromission (Springer, 1960; Tricas and LeFeuvre, 1985; Carrier *et al.* 1994). Biting also occurs in several species of batoid elasmobranchs during various stages of courtship and copulation. Male eagle rays *Aetobatis narinari* dive upon and gouge the back of females during courtship (Tricas, 1980). In the nuptial behaviour of the roughtail stingray *Dasyatis centroura*, the male bites the pectoral fin of the female and inflicts scars (Reed and Gilmore, 1981). Similar courtship and copulatory bites are also known for the round stingray *Urolophus halleri* (Nordell, 1994), the bullseye stingray *Urolophus concentricus* (McCourt and Kerstitch, 1980) and the cownose ray (Uchida *et al.* 1990).

Batoid teeth are classified as either molariform or plate-like (Moss, 1977). Molariform teeth occur in stingrays (Dasyatidae) and skates (Rajidae) and are used to grasp small prey. In contrast, the plate-like teeth of the Myliobatidae function to crush hard-shelled prey such as large bivalves and gastropods (Bigelow and Schroeder, 1953). Despite the adaptive functions of smooth teeth in rays for feeding, this shape is relatively ineffective for gripping the pectoral fins of females during mating. This additional reproductive function of male teeth has resulted in sexual dental dimorphism, which is hypothesized (but never demonstrated) to enhance the grip efficiency and ultimately to increase male reproductive success. Dental sexual dimorphism is widespread in batoids and has previously been assumed to be a static characteristic of tooth structure (Bigelow and Schroeder, 1953). It was first suggested that dental dimorphism may have evolved to allow the sexes to feed on different food items (Feduccia and Slaughter, 1974), but no evidence exists to support this hypothesis (McEachran, 1975; Taniuchi and Shimizu, 1993). Thus, while male teeth function in both feeding and mating, female teeth function only in feeding.

The continuous replacement of teeth throughout life (polyphyodonty) occurs in fishes, amphibians and reptiles and is best described in the Elasmobranchii (Moss, 1972). For species that bite during their courtship or mating and that also exhibit periodic reproductive seasonality, it should theoretically be advantageous for males to develop sharp, pointed teeth during the mating season to enhance reproductive success but then revert to the dentition more suited for feeding.

This study tested the hypothesis that polyphyodonty permits

periodic variation in tooth shape to enhance male reproductive success. We tested the hypothesis by (i) assessing monthly changes in tooth morphology correlated with breeding activity, (ii) determining tooth replacement rate between the sexes, and (iii) testing grip tenacity for the different tooth types. We chose the Atlantic stingray *Dasyatis sabina* as our model species because it feeds upon small benthic crustaceans, polychaetes and invertebrates associated with seagrass beds (Cook, 1994) and shows a well-defined mating period from October to May (Snelson *et al.* 1988; Maruska *et al.* 1996).

Materials and methods

Atlantic stingrays *Dasyatis sabina* (Lesueur) were collected monthly over a 24 month period, from March 1992 to February 1994 from the Banana River, Brevard County, Florida, USA. Individual rays were encircled and captured with a 6 m seine net, which avoided damage to their teeth. Rays were killed, placed on ice and transported to the laboratory. The jaw cartilages were removed, cleaned of connective tissue, rinsed with fresh water and air-dried at room temperature. The largest tooth on the labial margin of the palatoquadrate was extracted from each jaw. Teeth were extracted from the second tooth row, which exhibited less wear than teeth from the first tooth row. Teeth at this position were functional.

Each tooth was examined in lateral profile under a microscope, and a high-contrast image was captured *via* a video camera and digitally stored on a computer. Each tooth profile (ventral tooth root excluded) was imported into the image analysis program (NIH Image v1.55b). The centroid (geometric centre) was determined for each image and radial lines were drawn to the border at 2° increments in a counterclockwise rotation starting from the rostral horizontal vector (0°) (Fig. 1). Polar radii were converted to rectangular coordinates with vector angle as the ordinate, plotted on a Cartesian plane, and used as the primary variate in structure analysis.

To determine the rate of tooth replacement, stingrays were maintained in large, outdoor tanks with a constant flow-through of sea water at the Indian River Marine Science Research Center in Vero Beach, Florida, USA. Experiments were conducted from September to December 1993 and water temperature ranged from 29.5 to 21.0 °C with a mean of 24 °C. Each ray was marked by a plastic tag placed in either the pectoral or pelvic fin. The tags did not appear to affect the movement or behaviour of the fish. Rays were fed to satiation three times a week on a diet of live or frozen shrimp, clams, crabs and gastropods, which were presented whole within their shells.

Individual teeth were marked 2 days after the rays began to feed in captivity. To mark teeth, each ray was removed from the tank and placed on its back in a cushioned box partially filled with water. The mouth was held open and a depression (approximately 1 mm in diameter) was made with a dental burr in the largest tooth located in rows 2–4 lingual from the labial margin. Marked teeth were from the same position as teeth
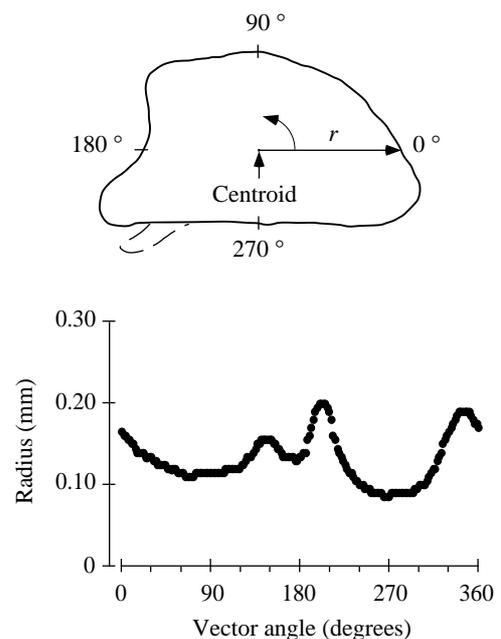

Fig. 1. Lateral profile of a *Dasyatis sabina* tooth demonstrating how tooth shape, described by polar coordinates, is converted to a line on a Cartesian plane. Lines are drawn from the centroid to the tooth margin at 2° intervals and the corresponding radius (r) is plotted against the vector angle to generate a curve on a Cartesian plane.

sampled for morphometric analysis. Care was taken to ensure that the dental burr did not disturb the tooth bed. Rays were returned to the holding tank and fed soon after the marking procedure. Marked teeth were examined a minimum of three times per week and their position within the jaw was recorded. When a marked tooth migrated out of the jaw, a new tooth was marked. A Student's *t*-test was used to compare the rate of tooth replacement between the sexes.

To determine bite force exerted by the rays, a strain gauge (Measurements Group Inc. EA-06-062TZ-350) was mounted on a thin (2 cm×2 cm) brass plate and the wire leads sealed with epoxy resin. Voltage across the strain gauge changed relative to force applied to the flexible brass substratum. Jaws removed from six males collected during the mating and non-mating seasons were dried, cast in a resin block base, and the upper and lower elements were mounted on a horizontal hinge. The strain gauge was placed between the hinged jaws, mass-loaded and the resulting voltage used to generate a force calibration curve. Male and female rays were captured alive and the strain gauge was positioned between the jaws. The introduction of the strain gauge produced a reflex biting action (Roberts and Witkovsky, 1975), which was recorded digitally at 0–5 kHz bandwidth. From the calibration curve, it was determined that a mass of 300 g (=2.94 N) closely approximated the peak bite force recorded for male stingrays.

To determine grip performance, pairs of upper and lower jaw elements were mounted on the horizontal hinge, positioned at a bite point 1 cm from the disk margin of a female pectoral fin, and mass-loaded at 300 g (2.94 N). The fin was then

Fig. 2. The tooth grip tenacity apparatus used to measure the force required to break the grip on the pectoral fin by the jaw. Paired hinge-mounted upper jaws (uj) and lower jaws (lj) were mass loaded (300 g) to approximate the force of a male stingray bite. A female pectoral fin was mounted on the force meter and displaced laterally from the jaws at a velocity (v) of 0.5 mm s^{-1}. The peak force (N) required to break the fin from the jaws was compared for male jaws from mating and non-mating seasons. It was found that teeth obtained during the mating season provided a much greater grip tenacity than teeth obtained during the non-mating season.
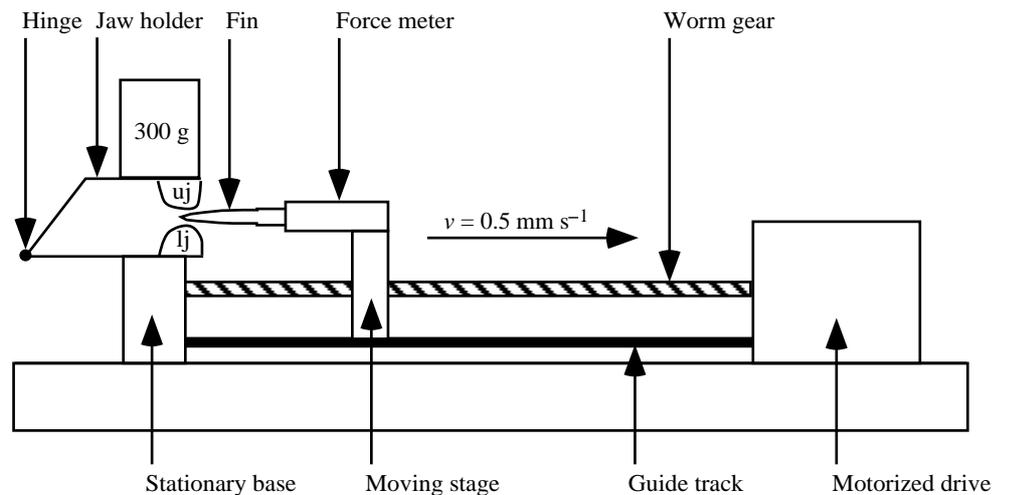
laterally displaced by a motorized test stand at a velocity of 0.5 mm s^{-1}, and the peak shear force required to break the grip was recorded using an Omega DFG-2 digital force gauge (Fig. 2). Peak forces for the molariform and cuspidate dentitions were assessed for homogeneity of variances and tested for differences using the Student's t-test.

Results

Teeth were examined from 167 males and 165 females. The mean disk width (maximum transverse body diameter) for males was 24.35±0.09 cm (S.E.M.) and for females was 27.29±0.16 cm (S.E.M.). Females were larger than males and the physical dimensions of their teeth were correspondingly greater.

A clear distinction in tooth shape is evident during the mating season between male and female *D. sabina* (Fig. 3). Male teeth are characterized by a sharp, caudally recurved cusp during October–June (Fig. 4), but are rounded and indistinguishable from female teeth (Fig. 5) during the non-mating months of July–September. During the mating season, the radius vector curve for male teeth shows a sharp peak at approximately 140° (Fig. 4). This describes the recurved cusp which is diagnostic of males during the mating season. A smaller peak (mean radius 0.132 mm) at approximately 230° describes the region at the caudal base of the tooth. An analysis of variance demonstrates that the maximum radius for males (at approximately 140°) changed over an annual cycle (F=13.109, P<0.001). A Tukey's test was used to determine which months differed (Table 1).

In contrast, female teeth show no variation in their molariform shape among all months of the study. The tooth radius vector curve for females is characterized by two peaks (Fig. 5). The first peak (mean radius 0.164 mm) occurs at approximately 140° and describes the caudal extreme of the functional grinding surface. The larger second peak (mean radius 0.214 mm) occurs at approximately 200° and describes the caudal base of the tooth. The maximum radius for females
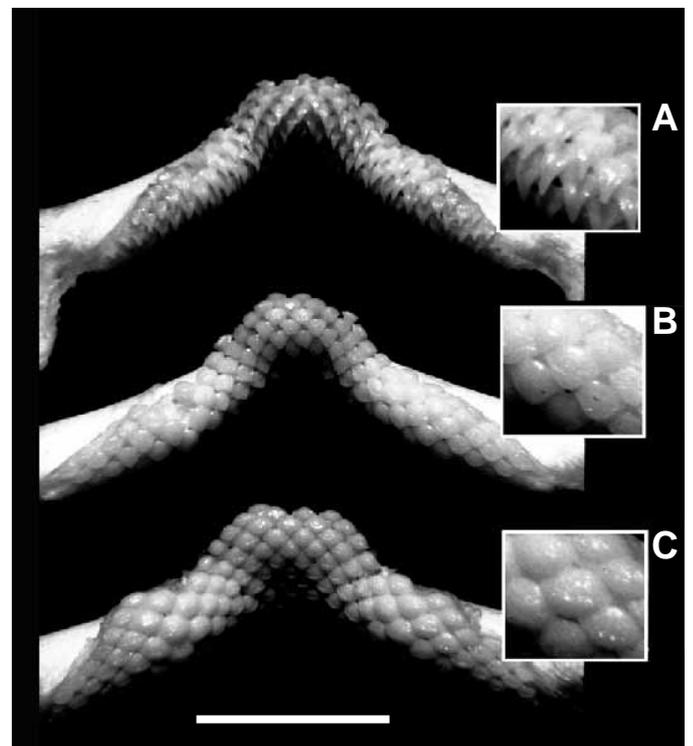

Fig. 3. Upper jaw dentition of a male stingray (*Dasyatis sabina*) sampled during the mating season (A). The cuspidate dentition is evident not only in the first 3–4 rows of functional teeth but also in the developing teeth beneath the dental membrane. In contrast, the upper jaw dentition of a male sampled during the non-mating season (B) is molariform and similar to the female dentition (C), which does not vary seasonally. Insets show enlarged views of the teeth. Scale bar, 1.0 cm.

does not differ (analysis of variance, ANOVA, F=0.976, P=0.471) over an annual cycle, indicating that female tooth morphology is constant.

The seasonal nature of the morphological change for males is best visualized with a stacked time series of curves over 24
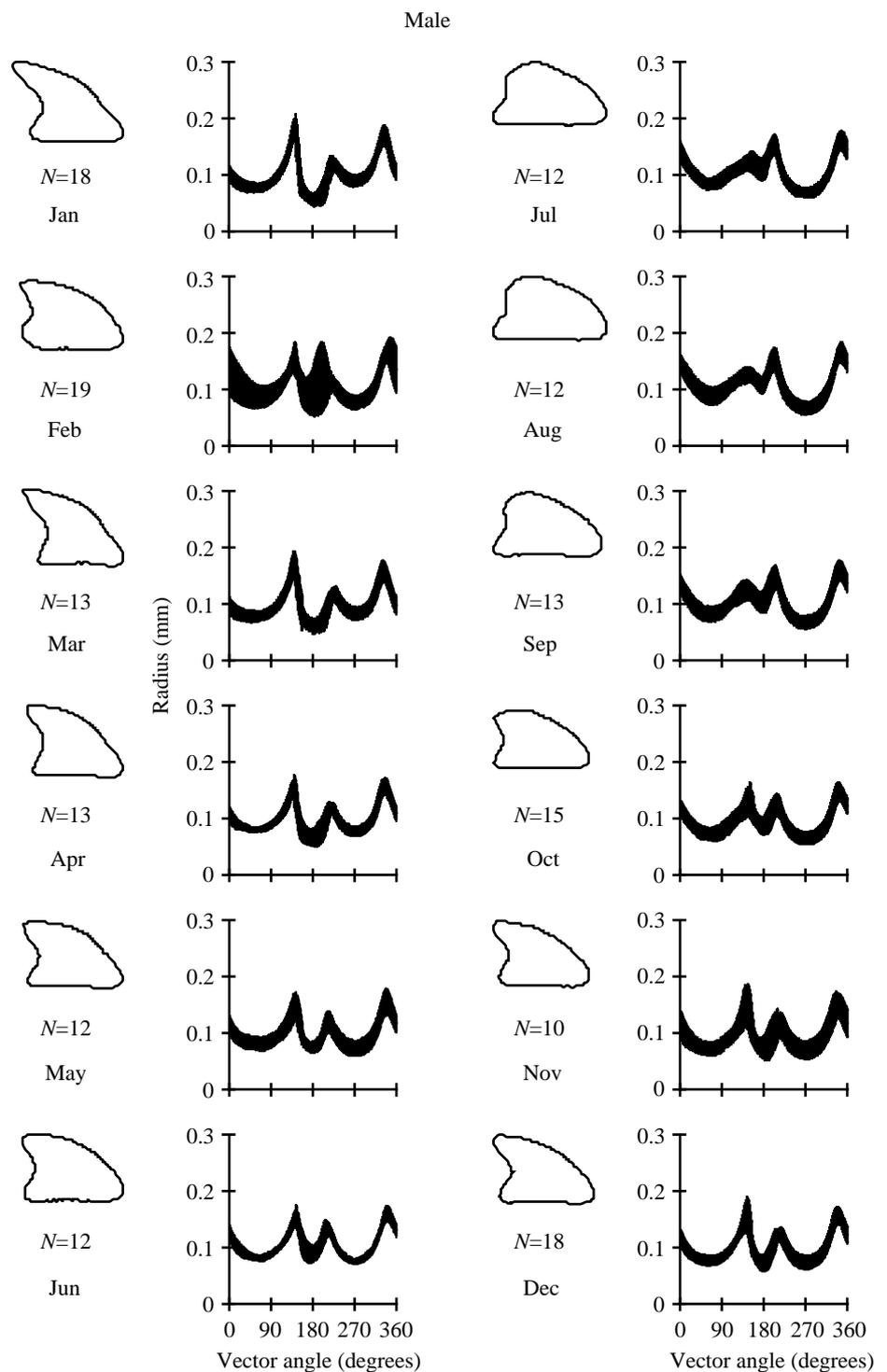
Male

Fig. 4. Tooth radii for 180 vectors (0–358° at 2° increments) from males sampled over 24 consecutive months and pooled into 12 one-month groups. The tooth profile for each month was generated by taking the mean value at each 2° interval from the Cartesian plot and converting it to polar coordinates. Data are plotted as a band bounded by ± 1 s.d. about the mean.

consecutive months (Fig. 6A). This illustrates the rise and fall of the 140° vector angle peak over time. Three peaks at approximately 140° are evident: (i) at the end of the mating season in spring 1992; (ii) during the mating season from winter 1992 to spring 1993; and (iii) at the start of the mating season in winter 1993–1994. These three mating season peaks are separated by two troughs during the non-mating seasons which correspond to the decreased radial length of the cusp.

The highly dynamic nature of the male dentition contrasts with the relatively static shape of the female dentition. A stacked time series plot for females shows little change in the shape of the curve over time, and the peak at 140° remains relatively stable (Fig. 6B). Female teeth are larger than male teeth and, consequently, the radii are of greater magnitude.

A principal components analysis of the tooth radii for each of 12 months (pooled from 24 months) shows clusters for
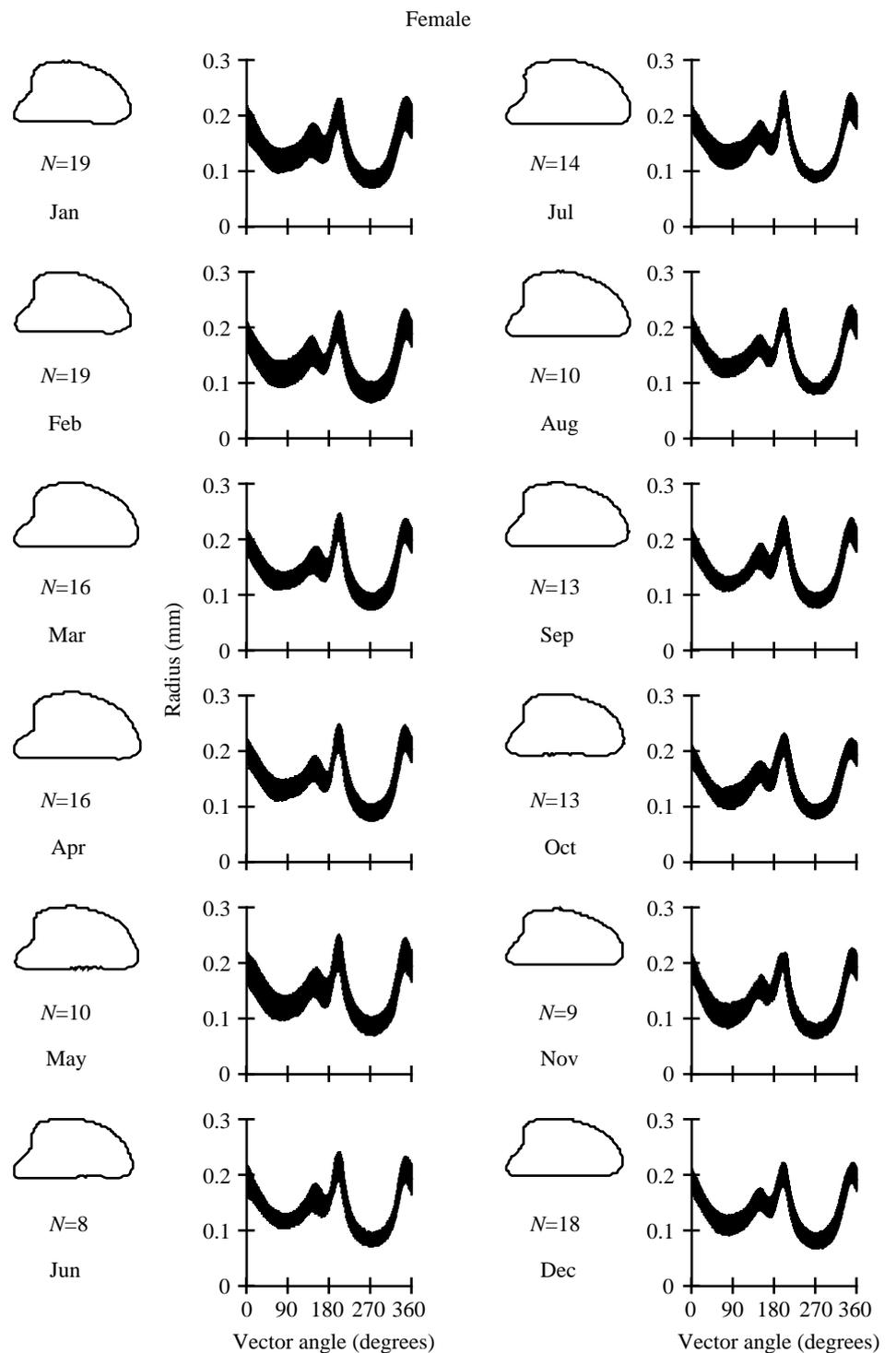
Female

Fig. 5. Tooth radii for 180 vectors (0–358° at 2° increments) from females sampled over 24 consecutive months and pooled into 12 one-month groups. The tooth profile for each month was generated by taking the mean value at each 2° interval from the Cartesian plot and converting it to polar coordinates. Data are plotted as in Fig. 4.

males discrete from females during the mating season, when the teeth are maximally dissimilar (Fig. 7). Male and female teeth do not cluster separately during the non-mating season. The clusters for males and females converge during the transitional month of June and diverge during the transitional month of October. An arch effect is evident which indicates that the relationship between the principal components may not be linear (Pielou, 1984).

To demonstrate that the phenomenon of increased cusp length during the mating season is not an artefact of a fish size sampling bias, mean disk width and mean maximum radius were plotted over an annual cycle (Fig. 8). The disk widths for both sexes were relatively constant over a year, as was the maximum tooth radius for females. The maximum tooth radius for males, however, increased at the onset of the mating season and decreased at the end. This demonstrates that, even though

Table 1. *Matrix of Tukey's tests showing differences in male tooth maximum radius over a 12 month period*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	–											
Feb	–	–										
Mar	–	–	–									
Apr	*	–	–	–								
May	**	–	–	–	–							
Jun	*	–	–	–	–	–						
Jul	***	***	***	**	**	**	–					
Aug	***	***	***	–	–	*	–	–				
Sep	***	***	***	*	–	*	–	–	–			
Oct	***	***	***	–	–	–	–	–	–	–		
Nov	***	–	–	–	–	–	*	–	–	–	–	
Dec	***	–	–	–	–	–	***	**	**	–	–	–

Teeth sampled in January were significantly different from those sampled in all other months except February and March; teeth sampled in July were significantly different from those sampled in all other months except August, September and October. – , not significant; *$0.01<P<0.05$; **$0.001<P<0.01$; ***$P<0.001$.

the size of the males remained the same, their teeth developed distinctly longer cusps during the mating season.

The mean tooth replacement rate for males was 5.6±0.86 days per tooth row (s.e.m.). For females, the mean tooth replacement rate was 7.4±1.17 days per tooth row (s.e.m.). A *t*-test revealed that the rate of tooth replacement did not differ between the sexes ($t=1.11$, $P=0.274$). The teeth were replaced more slowly when temperature briefly fell in the second and third weeks of October.

To test the grip efficiency hypothesis, the shear force required to dislodge a pectoral fin from the jaws was measured on specimens from males collected during mating and non-mating months. Peak bite force was measured from four living rays and ranged from 0.69 to 6.57 N with a mean of 2.05±0.72 N (s.e.m., $N=8$). We assumed the male bite force during gripping of a female would exceed the mean, and therefore used a 300 g (=2.94 N) load force on jaws taken from males and positioned at the lateral disk margin of a female pectoral fin. The break shear force was then determined. Jaws collected from rays in the mating season required a mean horizontal shear force of 0.77±0.09 N (s.e.m., $N=6$) to slip the pectoral fin from the jaw compared with a force of 0.45±0.17 N (s.e.m., $N=6$) for jaws during the non-mating season (two-sample *t*-test for unequal variances, $t=4.01$, $P=0.001$). Thus, sharp teeth require 58.4 % more shear force to release the fin from the jaw.

Discussion

Sharp cuspidate male dentition and smooth molariform female dentition are known for many batoid elasmobranchs (Bigelow and Schroeder, 1953). Previous studies have assumed the adult dental morphology to be static (McEachran, 1975; Taniuchi and Shimizu, 1993; Nordell, 1994); however, the present study demonstrates that tooth morphology in adult male stingrays is dynamic and periodic.

Male teeth from rays during the mating season have a gross morphology very different from the teeth of non-mating-season males or from female teeth at any time. The different functions of the male elasmobranch dentition, to feed and to grip females during mating, may require different optimal tooth morphologies. If cuspidate teeth were equally effective as molariform teeth for feeding, there would be no advantage to having a variable male dentition. The development by males of a female-like molariform dentition during the non-mating months is presumably advantageous for feeding. The diet of male and female *D. sabina* consists mostly of small crustaceans (amphipods, mysids, isopods) and polychaetes, with a shift by both sexes to the relatively heavily calcified brittlestar disks during the summer (Cook, 1994). Even though males and females possess a very different dentition for part of the year, their diet consists of the same prey items. It remains to be determined whether the molariform dentition common to both sexes at this time increases feeding efficiency on these hard-shelled prey organisms.

The results of the tooth replacement rate experiment are not consistent with the hypothesis that females replace their teeth at a slower rate than males, so that their pointed dentition is worn down, while the male dentition retains the pointed cusp. This wear hypothesis was suggested as an explanation for sexual dimorphism in skate teeth (Feduccia and Slaughter, 1974) but was later rejected by McEachran (1975). Although evidence of wear on some teeth of *D. sabina* was visible, it was not sufficient to grind down the hard, mineralized cusp. Further evidence to refute the wear hypothesis comes from our examination of pre-emergent teeth. During the transitional months at the end of the mating season, male pre-emergent replacement teeth are molariform, while the functional teeth are cuspidate. Furthermore, pre-emergent teeth are pointed during the transition from the non-mating to the mating season. This demonstrates that tooth morphology is determined prior to emergence and is not a function of differential wear.

Although many studies have experimentally determined tooth replacement rate in sharks (Ifft and Zinn, 1948; Applegate, 1967; Moss, 1967, 1972; Boyne, 1970; Wass, 1973; Reif *et al.* 1978; Luer *et al.* 1990), to our knowledge this is the first study to describe tooth replacement in a batoid. The data
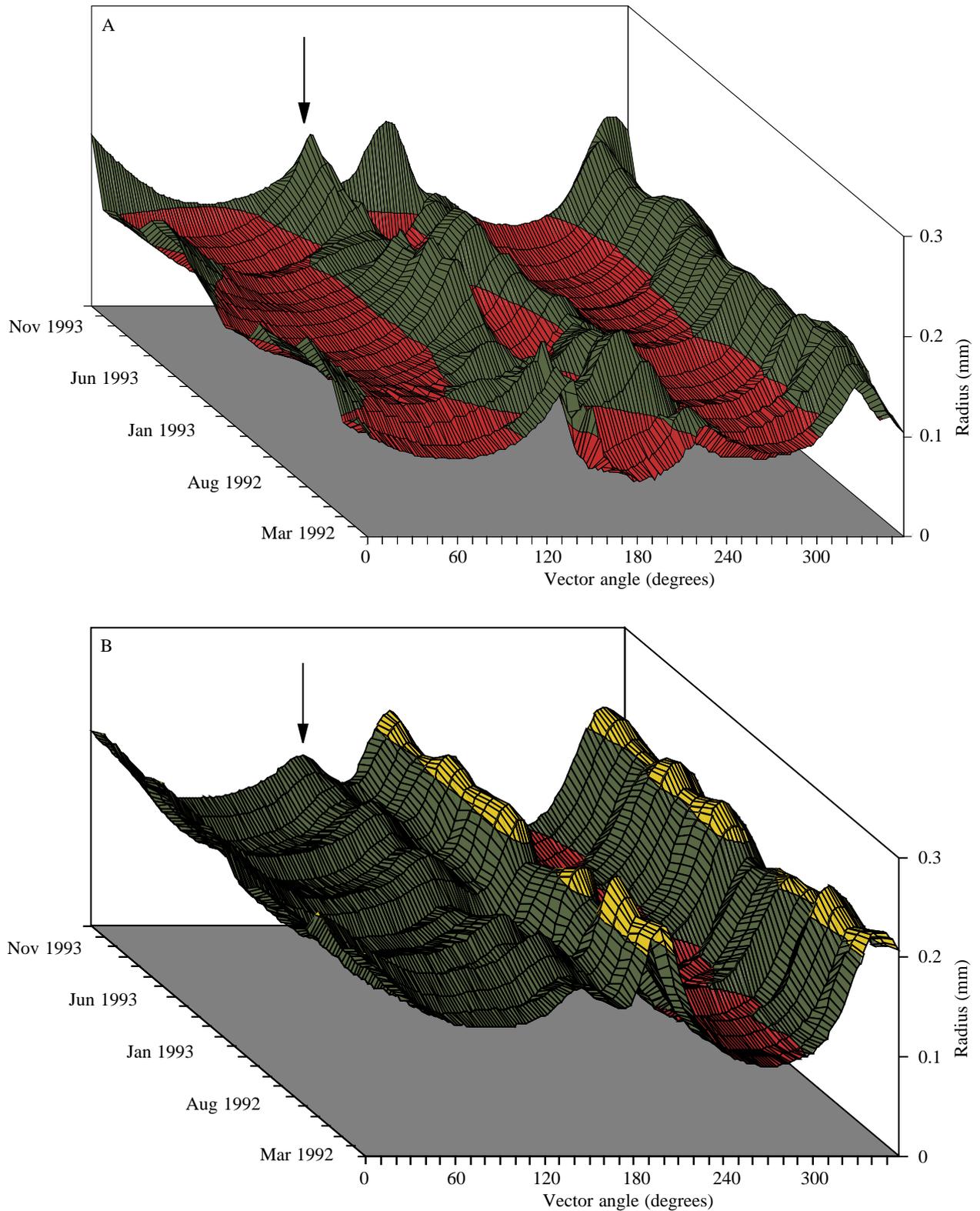
Fig. 6. (A) Three-dimensional surface plot of male tooth radius *versus* vector angle over 24 months from March 1992 to February 1994. Peak tooth radii are found during the mating season (October–May) and in June at a vector angle of approximately 140° (arrow). The maximum radii are separated by non-mating season (June–September) troughs where the teeth have a similar morphology to those of females. (B) Three-dimensional surface plot of female tooth radius *versus* vector angle over 24 months from March 1992 to February 1994. The curve for females shows comparatively little change in tooth radius at 140° (arrow) between the mating and non-mating seasons.
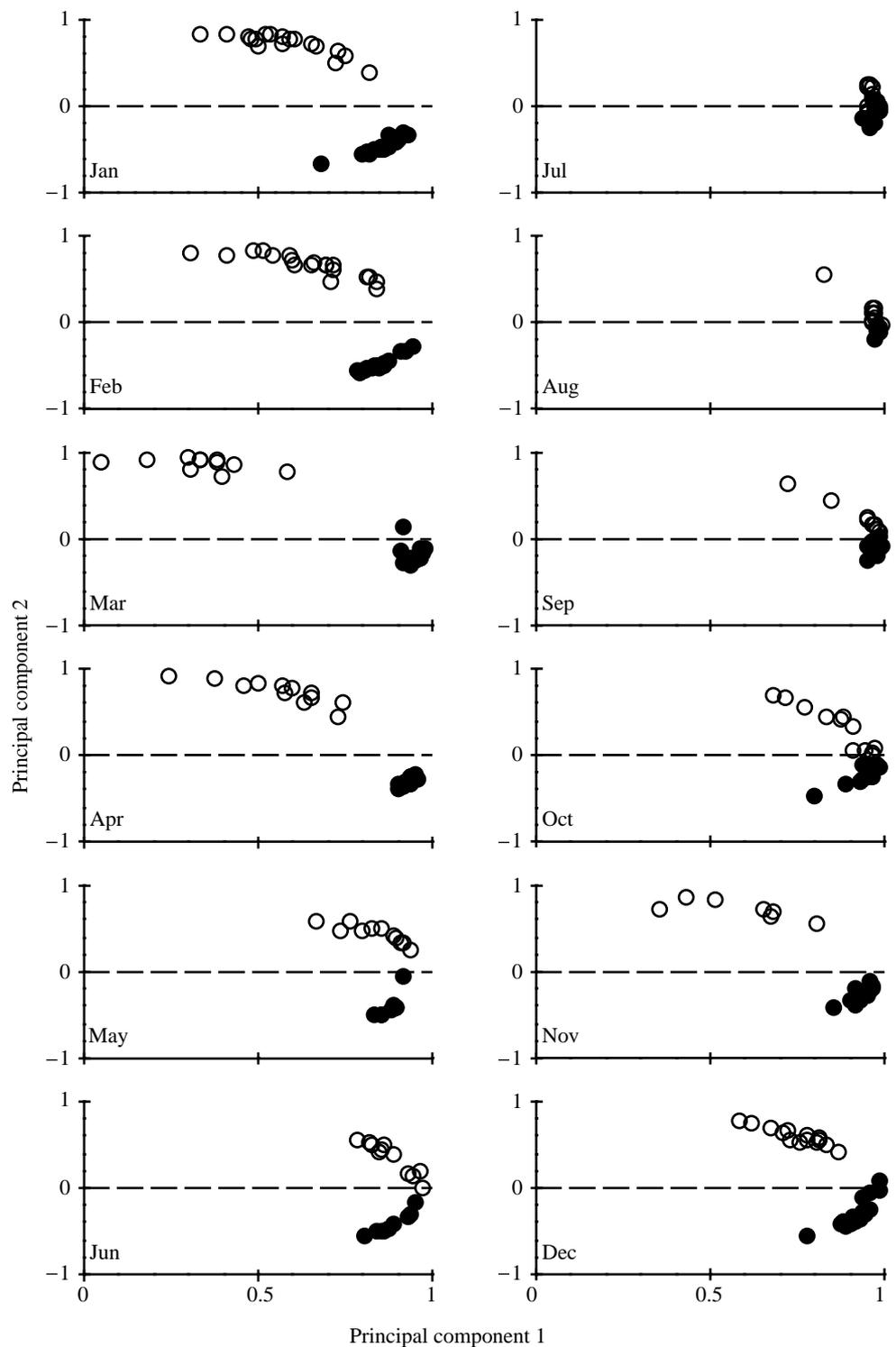
Fig. 7. The principal components analysis illustrating how male (○) and female (●) teeth cluster separately during the mating season (October–May) and in June but are morphologically indistinguishable during the non-mating season (June–September). In the transitional months, the teeth demonstrate varying degrees of separation.

for *D. sabina* indicate a replacement rate of 5–7 days per tooth row, at approximately 24 °C, which is sufficient to allow replacement of the entire tooth set within the October–May period of mating activity. Given a tooth replacement rate of 5–7 days per tooth row and 6–10 rows of replacement teeth, it would take 1–2 months to replace all the teeth present in the jaw. This is based on the replacement rate we determined during September–December, which includes the period when male

teeth are in transition from the molariform to the cuspidate morphology. Replacement rates are probably slower during the colder winter months. During the spring, when water temperature is initially lower, tooth replacement rate may be slower, and hence a protracted period may be required for the emergence of molariform teeth. It would be interesting to maintain rays over an entire year to determine how replacement rate varied with season.
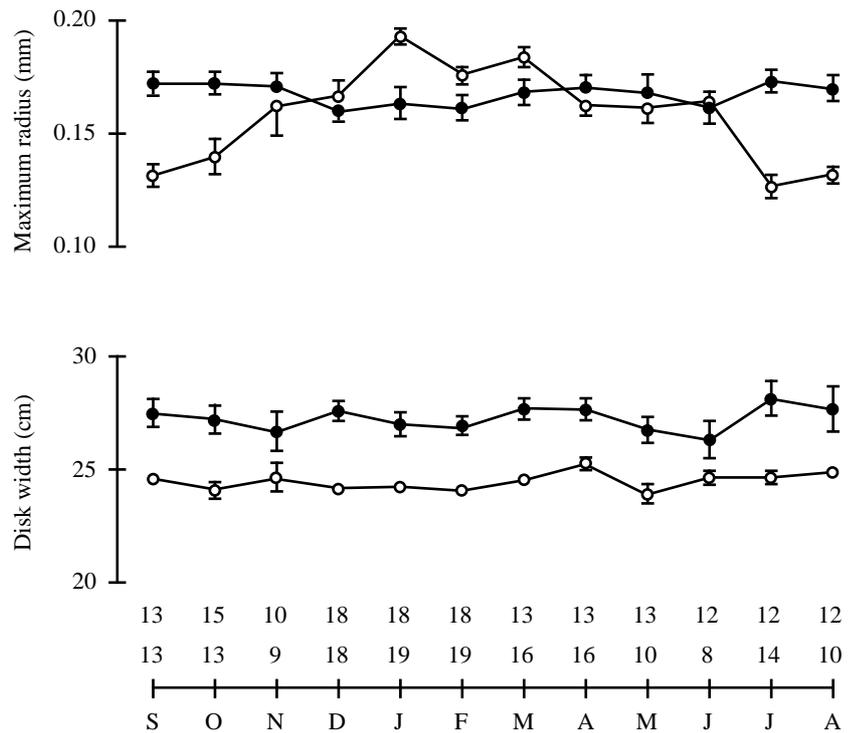
Fig. 8. Maximum tooth radius (see Fig. 1) for males (○) increases during the mating season but remains constant for females (●) (A). This phenomeon is not due to a size sampling bias as the disk width (maximum transverse body diameter) for both sexes remains constant over the same period (B). Sample sizes are given above the months for males (top) and females (bottom). Values are means ± s.e.m.

The 1–2 month lag between the initiation of tooth transition and when they assume a functional position correlates well with data on testis development and mating season (Maruska *et al.* 1996; Snelson *et al.* 1988). The testes reach their maximum size between September and October (Maruska *et al.* 1996), which is when mating activity begins. Further studies of pre-emergent tooth development patterns, associated changes in the supporting tissues and hormone cycling, are necessary to determine whether the induction of male dental dimorphism is regulated by reproductive hormones.

The grip tenacity experiments clearly demonstrate that the sharp dentition of males provides a better surface with which to maintain a grip on the pectoral fins of females. Fin gripping is an essential part of courtship and mating in nearly all elasmobranch fishes. Female rays and sharks appear reluctant to mate and often flee from courting males. Biting is thought to function as a pre-copulatory releasing mechanism by which males elicit females to cooperate during copulation (Springer, 1960). Once the claspers are inserted into the female, copulation may last for many minutes (Nordell, 1994). Thus, the periodic development of a cuspidate dentition may increase the number of successful male copulations and ultimately their reproductive success.

The dentition of other male batoids may also change during the mating season in order to maximize reproductive success. Dental sexual dimorphism is well documented in many batoids (Bigelow and Schroeder, 1953), and seasonal changes may be common. Although more subtle dental dimorphisms are known in sharks (Compagno, 1988), the possibility of periodic changes remains to be demonstrated. We predict that periodic dental dimorphism should be most prominent in species with mating and courtship behaviours that require vigorous grasping by the male for successful copulation.

In addition to extant elasmobranchs, the fossil shark and ray record should also be interpreted with attention to the possibility of periodic dental dimorphism in a single species. Elasmobranch phylogenies are typically constructed for extinct species on the basis of the few hard parts, usually the teeth, existing in the fossil record (Compagno, 1988). The gross differences in the male dentition of stingrays in the present study indicate that dental taxonomy could potentially result in the description of more than one species on the basis of teeth from different times of the year. Furthermore, serial tooth replacement is well known in teleost fishes (Norris and Prescott, 1959; Mochizuki and Fukai, 1983). Thus, other fishes may also exhibit seasonal dental dimorphism, driven perhaps by seasonally available prey or other unknown reproductive functions of the dentition in extinct species. The results of this work may also be relevant to other polyphyodontic vertebrates. Reptiles and amphibians also replace their teeth, and in some species males bite females during mating (Promislow, 1987). The results of this study open many other avenues for further studies on the dynamic functional morphology of the dentition in organisms which exhibit polyphyodonty.

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