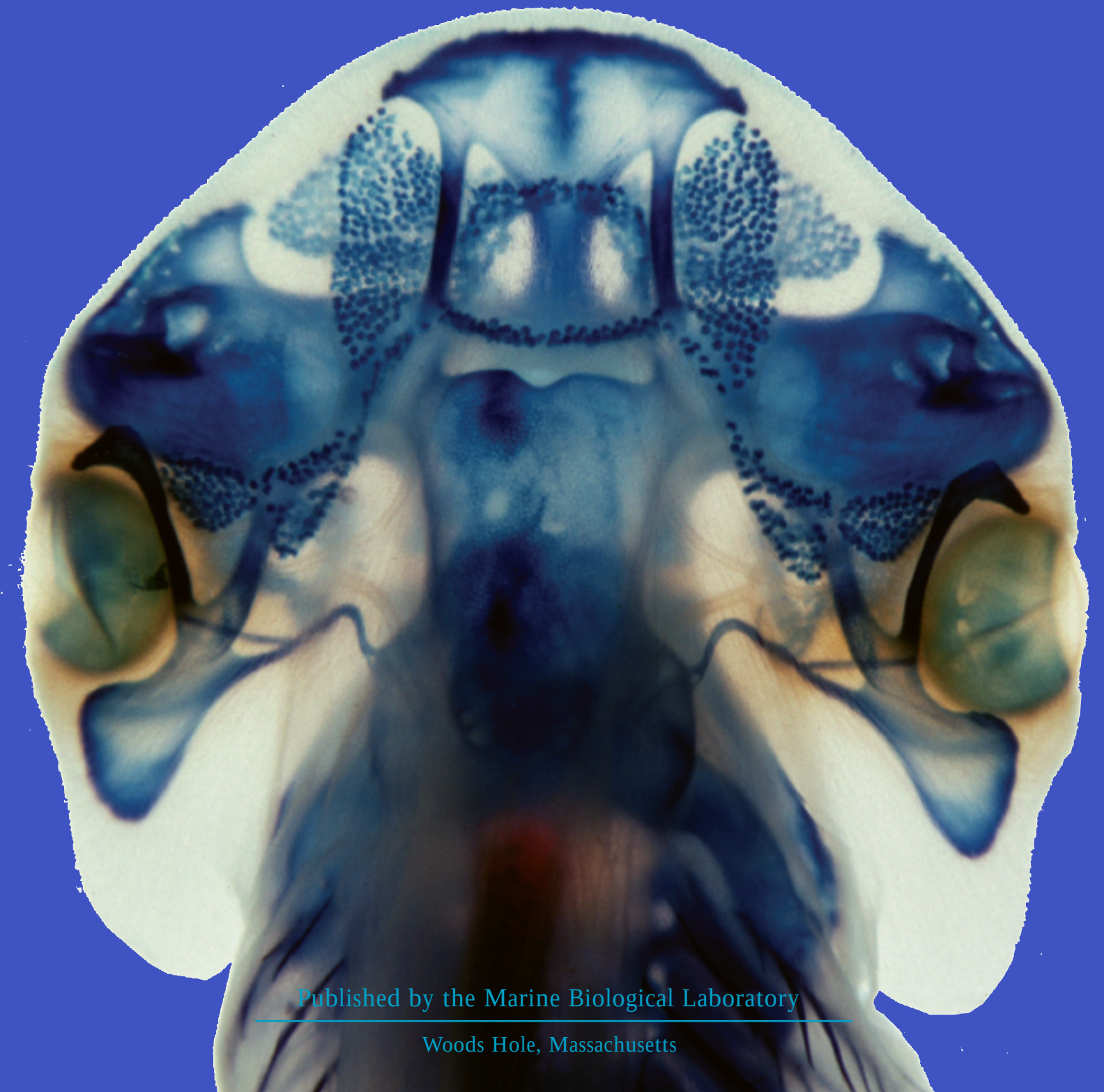
August 2005

Volume 209 • Number 1

THE BIOLOGICAL BULLETIN



Published by the Marine Biological Laboratory

Woods Hole, Massachusetts

Reference: *Biol. Bull.* **209:** 1–5. (August 2005)
© 2005 Marine Biological Laboratory

The Sexually Dimorphic Cephalofoil of Bonnethead Sharks, *Sphyrna tiburo*

STEPHEN M. KAJIURA[1,*], JOHN P. TYMINSKI[2], JESICA B. FORNI[3], AND ADAM P. SUMMERS[3]

[1] *Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, Florida 33431;* [2] *Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236; and* [3] *Ecology & Evolution, University of California, 321 Steinhaus Hall, Irvine, California 92697*

Sexually dimorphic head shape is common in vertebrates from teleosts to mammals. Herein we document that cephalic sexual dimorphism is also found in the cartilaginous fishes (Chondrichthyes). Male bonnethead sharks develop a prominent bulge along the anterior margin of the cephalofoil at the onset of sexual maturity. This contrasts with the uniformly rounded anterior margin of adult females and juveniles and embryos of both sexes. The anterior cephalic bulge is produced by elongation of the rod-like rostral cartilages, and its appearance corresponds temporally with the elongation of the rod-like cartilages of the male intromittent organs (claspers). We propose that the rostral cartilage elongation is a byproduct of endocrinological changes at the onset of sexual maturity that stimulate growth of the clasper cartilages. The basal location of the chondrichthyan fishes within the vertebrate clade extends the earliest appearance of cephalic sexual dimorphism among the vertebrates.

Vertebrate sexual dimorphisms are often expressed as differences in head morphology. Familiar examples include the hypertrophied brow of male gorillas (1, 2), prominent feather crests in numerous bird species, and the larger head of male skinks (3). Differences in head morphology are especially prevalent among the teleost fishes. Mature male dolphinfish, *Coryphaena hippurus,* possess a prominent bony crest on the anterior margin of the head (4), and the male humphead wrasse, *Coris aygula,* is characterized by a distinct forehead hump not found in females (5). Prior to spawning, males of several Pacific salmon species (*Oncorhynchus* spp.) develop dramatically different head morphologies from females; and during the mating season, many male cyprinids develop nuptial tubercles on their head (6). This synoptic list illustrates that sexual dimorphisms in head shape are both widespread and diverse.

Cartilaginous fishes (Chondrichthyes) exhibit a variety of sexual dimorphisms. These include differences in external reproductive anatomy—males possess elongate intromittent organs (claspers) whereas females do not; differences in size—females are often larger than males (7, 8); differences in tooth morphology—many male batoids possess cuspidate teeth to grip their female mates during courtship and copulation (9–11); and differences in skin thickness—some female sharks and rays possess a significantly thicker dermis than males (12, 13).

Herein we document a previously overlooked sexual dimorphism in a well-studied shark species, *Sphyrna tiburo* (Linnaeus, 1758), the bonnethead shark. Bonnethead sharks are small, coastal hammerhead sharks (Sphyrnidae) from the most speciose shark order, Carcharhiniformes, and are distributed along both the Atlantic and Pacific coasts of North and South America (7). They are characterized by a broadly rounded, spade-like head (Fig. 1a) and have the least degree of lateral head expansion of all sphyrnid species (7). The bonnethead sharks used in this study were all incidental mortalities collected by long line and gill net sets at various locations throughout coastal Florida and the Florida Keys. Individuals were categorized into three developmental stages based upon total length (TL): embryos, < 32 cm TL; juveniles, 32 to 58 cm TL; and adults, > 69 cm TL. Adults were separated from juvenile sharks on the basis of the total length at which the claspers on the male shark begin to dramatically elongate at the onset of sexual maturity (Fig. 1b). Individuals within the range of 58 to 69 cm

Received 3 February 2005; accepted 9 June 2005.
* To whom correspondence should be addressed. E-mail: kajiura@fau.edu

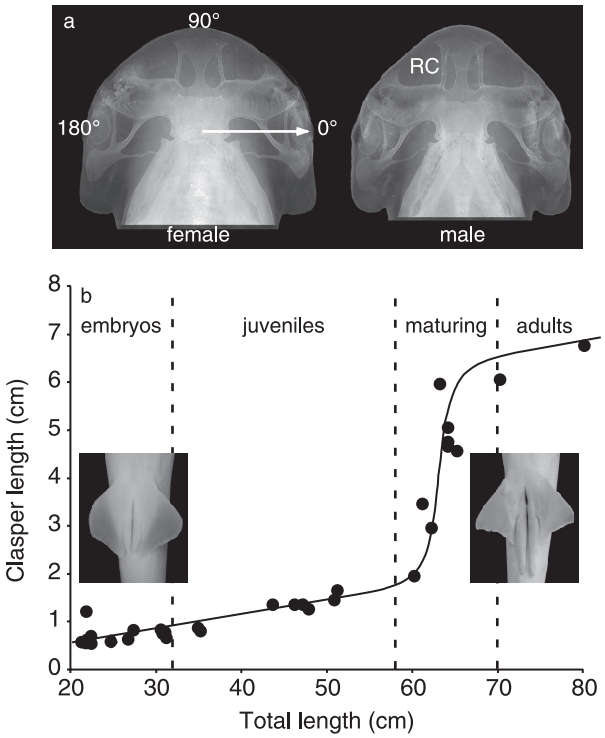


Figure 1. (a) Dorsal view, with radiographic overlay, of the cephalofoil of adult female (left) and male (right) bonnethead sharks. The broadly rounded anterior margin of the female cephalofoil contrasts with the distinct bulge along the anterior margin of the cephalofoil of the males. Radiographs reveal that the bulge found in the males is formed by the elongation of the medial and lateral rostral cartilages (RC). The rostral cartilage elongation corresponds temporally with the elongation of the clasper cartilages. (b) Clasper length plotted against total length for a subset of male bonnethead sharks used in this study. Clasper length increases dramatically at sexual maturity over a small range of shark size. Inset photographs highlight the difference in clasper size between embryonic and adult sharks. To quantify the difference in head shape between the sexes it was necessary to generate landmarks along the rounded anterior margin of the cephalofoil. The heads were severed in the transverse plane at the posterior margin of the lower jaw cartilages. A digital camera was used to photograph the dorsal surface of each head against a monochromatic background with a ruler scale within frame. Image analysis software (NIH Image ver. 1.63) was employed to generate an outline of the dorsal surface of the head and determine the position of the centroid. The radial distance from the centroid to the anterior margin of the head was measured at 4° increments from 0° at the level of the right eye to 180° at the level of the left eye (a) (*cf.* 11). These coordinates (vector angle, radius length) were then used as landmarks in a Procrustes superimposition analysis. We used only freshly frozen specimens for the analysis because preserved specimens might have introduced shrinkage artifacts.

TL were considered maturing and were excluded from analysis.

To determine whether the sexes can be distinguished on the basis of head morphology, we generated nonhomologous semi-landmarks (*sensu* 14) (Fig. 1a) that were subjected to a Procrustes superimposition analysis (15, 16). A Procrustes analysis (least-squares orthogonal mapping) is a technique for comparing two sets of data, in this case males and females, by using matching corresponding landmarks from each of the two data sets. The landmark coordinates from all individuals of one sex within a size class were used to generate a mean "consensus model" of a head. The method consists of minimizing the sum of the squared deviations by translating, rotating, and scaling the landmarks of one configuration (males) to match the other (females). The resultant deviations between corresponding landmarks are vector residuals that were subjected to a principal components analysis to determine whether the two configurations differed significantly from each other. The limitation of this technique was that we were forced to employ semi-landmarks to describe the outline of the head because distinct biologically derived landmarks along the anterior margin were lacking. The semi-landmarks were mutually correlated and provided a biased estimate of shape diversity by virtue of their reduced variability. Despite that limitation, we found significant differences in head shape for the adult size class.

The Procrustes analysis was repeated for each of the three size classes. A plot of the residuals on the first two principal component axes reveals that there is complete overlap in the head shape of embryonic male and female bonnethead sharks (Fig. 2a). The first two principal components account for 78.2% of the variation, and there is no significant difference in head shape between the sexes ($F_{2,26} = 0.065$, $P = 0.9376$). The juvenile bonnetheads also show overlapping distributions for the sexes, with the first two principal components accounting for 71.2% of the variation, and again, no significant difference in head shape between the sexes ($F_{2,28} = 0.671$, $P = 0.5193$) (Fig. 2b). In contrast to the earlier developmental stages, the adult bonnethead sharks demonstrate a clear separation between the sexes on the first two principal component axes (Fig. 2c). The difference in head shape is highly significant between the sexes ($F_{2,58} = 135.423$, $P < 0.0001$), and the first two principal components account for 86.6% of the variation. The absolute length of the rostral cartilages did not differ significantly between the sexes across a full range of sizes from embryos to adults (Fig. 3) (ANCOVA: $F_{1,85} = 1.097$, $P = 0.2980$). When tested among adults only, rostral cartilage length still failed to demonstrate a significant difference between the sexes (ANCOVA: $F_{1,34} = 0.855$, $P = 0.3617$). However, when rostral cartilage length as a percentage of total length was compared between the sexes, males had proportionally longer rostral cartilages than females (ANOVA: $F_{1,37} = 42.878$, $P < 0.0001$).

This study is the first report of a sexual dimorphism in head shape for any shark species. The distinct bulge that develops at maturity along the anterior median margin of the cephalofoil in male bonnethead sharks is caused by elongation of the three rostral cartilages (Fig. 1a). Because there is no significant difference in head shape between the sexes in embryonic and juvenile sharks, the difference in adults can likely be attributed to a developmental event linked to reproductive maturity.

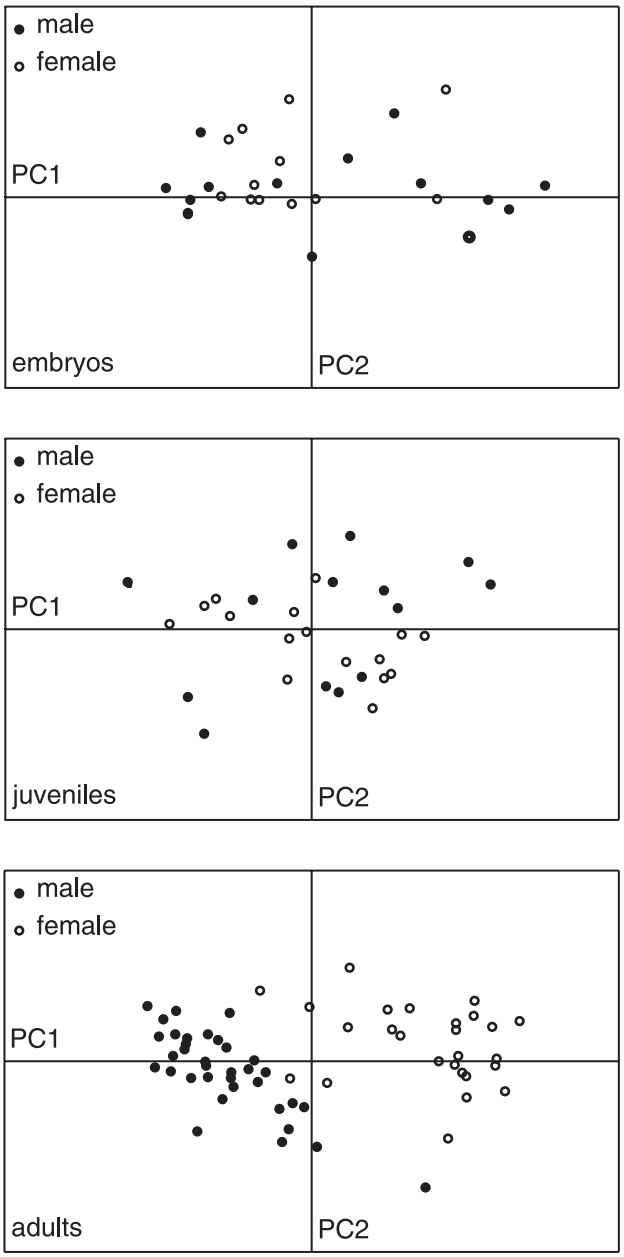


Figure 2. The results of a principal components analysis of the landmark coordinates (vector angle, radial length) for male and female bonnethead sharks. Males and females demonstrate significant overlap in their distribution for (a) embryonic and (b) juvenile sharks, whereas (c) adults clearly separate by sex.

At sexual maturity, the claspers of male chondrichthyan fishes, including bonnethead sharks, elongate dramatically (17, 18). The claspers are modifications of the pelvic fins and are composed of cartilaginous elements that form a tube for the transfer of sperm into the reproductive tract of the female (19). The elongation of the clasper cartilages at maturity corresponds temporally with the elongation of the rostral cartilages. We propose that the same mechanism responsible for stimulating the growth of the clasper cartilages has a secondary effect upon other long, thin cartilaginous elements. This elongation of rod-like cartilages could be mediated by either increased hormone production or the up-regulation of receptors for hormones involved in cartilage growth, although neither mechanism has yet been documented for *S. tiburo* (18).

The fact that the absolute value of the medial rostral cartilage length did not differ between the sexes is not surprising. Whereas male bonnethead sharks have relatively longer rostral cartilages, the males are smaller than females (20, 21), thus masking differences in the absolute length of the rostral cartilages. The highly significant difference between the sexes revealed by the Procrustes analysis demonstrates the power of that technique to detect subtle differences in shape. Because the Procrustes analysis is based upon numerous landmarks, it also indicates that the sexual dimorphism is characterized by a suite of changes along the anterior margin of the cephalofoil rather than by any single metric.

It is unlikely that the male cephalic bulge plays a functional role. Whereas the lateral expansion of the hammerhead shark head confers advantages for detection of prey *via* the electrosensory (22, 23) and olfactory systems (24), the anterior cephalic bulge is relatively subtle and is unlikely to exert a strong selective pressure. Rather, it appears that the cephalic bulge is merely a secondary sexual characteristic produced as a byproduct of changes in the endocrine system at the onset of sexual maturity. Alternatively, a large cephalic bulge may be an honest indicator of the endocrinological health of the male. If mate choice is exercised by female bonnethead sharks, the cephalic bulge may be selected *via* sexual selection akin to the type of selection that occurs in female guppies that prefer to mate with the males who possess the largest tails (25). However, because the cephalic bulge is rather subtle, a more direct indicator would be the size of the claspers.

The rostral cartilage elongation and consequent change in male head shape may have an effect on the feeding apparatus. Although we did not photograph or quantify the shape of the mouth, the cartilaginous jaw elements may also change concomitantly with the onset of sexual maturity in the males.

The smoothly rounded shape of the bonnethead shark cephalofoil highlights the rostral bulge seen in adult males. Although no other shark species has been shown to exhibit a cephalic sexual dimorphism, this may be due to the difficulty of detecting an increase in the length of the rostral cartilages in species with pointed snouts. Careful measurement of the heads of other shark species may reveal that rostral cartilage elongation at sexual maturity, with concomitant changes in head shape, is a widespread phenomenon among cartilaginous fishes.

Acknowledgments

We thank D. Adams for supplying heads from eastern Florida. We thank R. Hueter, J. Gelsleichter, J. Morris, M.

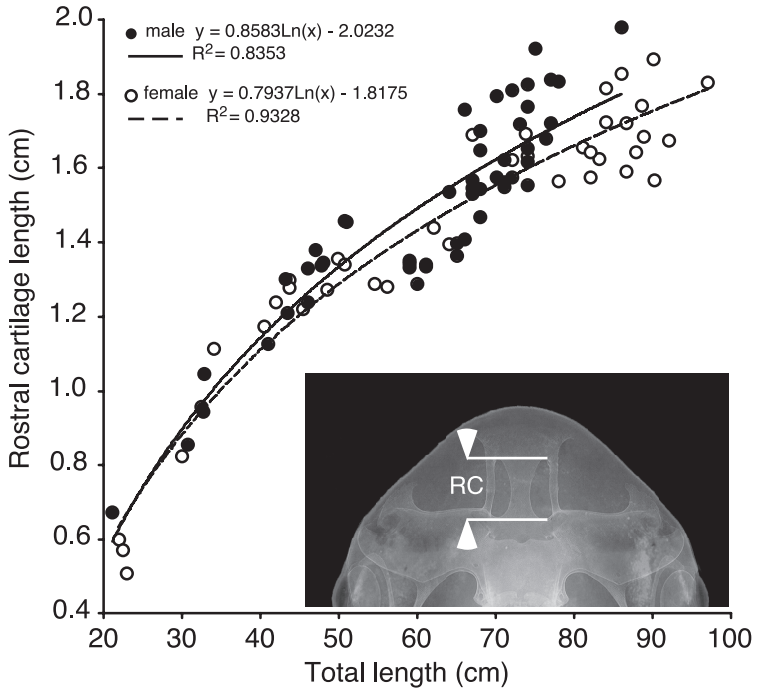


Figure 3. A subsample of bonnethead shark specimens—embryos to adults of both sexes—was x-ray imaged, and the length of the medial rostral cartilage (RC) was measured. An analysis of covariance, with total length of the shark as covariate, was employed to determine if rostral cartilage length differed significantly between the sexes.

Amato, C. Manire, and various Mote Marine Laboratory interns and staff for providing support and additional shark samples from throughout Florida. This work was supported in part by grants from the McDowell Foundation and the National Science Foundation to APS, and by NOAA/NMFS grants in support of the Center for Shark Research and the National Shark Research Consortium.

Literature Cited

1. **Sakka, M. 1986.** Sexual dimorphism in great apes: the skull of the gorilla. *Symp. Soc. Study Hum. Biol.* **24:** 79–103.
2. **O'Higgins, P., W. J. Moore, T. J. McAndrew, and R. M. Flinn. 1990.** Patterns of cranial sexual dimorphism in certain groups of extant hominoids. *J. Zool.* **222:** 399–420.
3. **Vitt, L. J., and W. E. Cooper, Jr. 1985.** The evolution of sexual dimorphism in the skink *Emeces laticeps:* an example of sexual selection. *Can. J. Zool.* **63:** 995–1002.
4. **Palko, B. J., G. L. Beardsley, and W. J. Richards. 1982.** Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Corphaena equiselis* Linnaeus. *NOAA Tech. Rep. NMFS Circ.* **443.**
5. **Allen, G. 1997.** *Marine Fishes of Tropical Australia and South-east Asia.* Western Australia Museum, Perth. 292 pp.
6. **Scott, W. B., and E. J. Crossman. 1985.** *Freshwater Fishes of Canada.* Fisheries Research Board of Canada, Ottawa. 966 pp.
7. **Compagno, L. J. V. 1984.** FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. *FAO Fish. Synop.* **125, Vol. 4, Part 2:** 251–655.
8. **Carlson, J. K., and G. R. Parsons. 1997.** Age and growth of the bonnethead sharks, *Sphyrna tiburo,* from northwest Florida, with comments on clinal variation. *Environ. Biol. Fishes* **50:** 331–341.
9. **McCourt, R. M., and A. N. Kerstitch. 1980.** Mating behavior and sexual dimorphism in dentition in the stingray *Urolophus concentricus* from the Gulf of California. *Copeia* **1980:** 900–901.
10. **Taniuchi, T., and M. Shimizu. 1993.** Dental sexual dimorphism and food habits in the stingray *Dasyatis akajei* from Tokyo Bay, Japan. *Nippon Suisan Gakkaishi* **59:** 53–60.
11. **Kajiura, S. M., and T. C. Tricas. 1996.** Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray, *Dasyatis sabina. J. Exp. Biol.* **199:** 2297–2306.
12. **Pratt, H. L., Jr. 1979.** Reproduction in the blue shark, *Prionace glauca. Fish. Bull.* **77:** 445–470.
13. **Kajiura, S. M., A. P. Sebastian, and T. C. Tricas. 2000.** Dermal bite wounds as indicators of reproductive seasonality and behaviour in the Atlantic stingray, *Dasyatis sabina. Environ. Biol. Fishes* **58:** 23–31.
14. **Bookstein, F. L. 1997.** Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Med. Image Anal.* **1:** 225–243.
15. **Rohlf, F. J., and D. Slice. 1990.** Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* **39:** 40–59.
16. **Goodall, C. 1991.** Procrustes Methods in the Statistical Analysis of Shape. *J. R. Stat. Soc.* **53:** 285–339.
17. **Parsons, G. R. 1993.** Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo. Environ. Biol. Fishes* **38:** 25–35.
18. **Gelsleichter, J. G., L. E. L. Rasmussen, C. A. Manire, J. Tyminski, B. Chang, and L. Lombardi-Carlson. 2002.** Serum steroid concentrations and development of reproductive organs during puberty in male bonnethead sharks, *Sphyrna tiburo. Fish Physiol. Biochem.* **26:** 389–401.
19. **Wourms, J. P. 1977.** Reproduction and development in chondrichthyan fishes. *Am. Zool.* **17:** 379–410.
20. **Gelsleichter, J., B. G. Steinetz, C. A. Manire, and C. Ange. 2003.**

Serum relaxin concentrations and reproduction in male bonnethead sharks, *Sphyrna tiburo. Gen. Comp. Endocrinol.* **132:** 27–34.

21. **Lombardi-Carlson, L. A., E. Cortes, G. R. Parsons, and C. A. Manire. 2003.** Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo,* (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Mar. Freshw. Res.* **54:** 875–883.
22. **Kajiura, S. M. 2001.** Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. *Environ. Biol. Fishes* **61:** 125–133.
23. **Kajiura, S. M., and K. N. Holland. 2002.** Electroreception in juvenile scalloped hammerhead and sandbar sharks. *J. Exp. Biol.* **205:** 3609–3621.
24. **Kajiura, S. M., J. B. Forni, and A. P. Summers. 2005.** Olfactory morphology of carcharhinid and sphyrnid sharks—does the cephalofoil confer a sensory advantage? *J. Morphol.* **264:** 253–263.
25. **Bischoff, R. J., J. L. Gould, and D. I. Rubenstein. 1985.** Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **17:** 253–256.