



Range, sexual dimorphism and bilateral asymmetry of rostral tooth counts in the smalltooth sawfish *Pristis pectinata* Latham (Chondrichthyes: Pristidae) of the southeastern United States

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Abstract

Rostral tooth counts of *Pristis pectinata* specimens from museum collections, research surveys, and fisheries activities were examined to provide information on sexual dimorphism, bilateral asymmetry, and to aid in the resolution of the taxonomic uncertainty that surrounds the Pristidae. Counts were taken from 105 smalltooth sawfish captured in Florida and Georgia, USA, from 1834 to 2007. The number of rostral teeth present was 22 to 29 per side and 45 to 56 in total. These counts were more constrained, and mean values lower, than historically reported for this species in the literature. *Pristis pectinata* rostral tooth counts exhibited sexual dimorphism, with males on average having more rostral teeth than females. Bilateral asymmetry in rostral tooth counts was displayed in 73% of individuals, with no consistent side on which the greatest count occurred. No significant difference between left and right side rostral tooth counts was found.

Key words: rostral teeth, endangered species, systematics, taxonomy

Introduction

Seven species of sawfish are currently recognized worldwide (Compagno 1999, 2005) and all are considered critically endangered by the World Conservation Union (IUCN 2006). All species are protected from international trade under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I, except for *Pristis microdon* which is protected under Appendix II. In the USA *P. pectinata*, the smalltooth sawfish, was once distributed throughout the Gulf of Mexico and along the Atlantic coast (Bigelow & Schroeder 1953). However, decades of capture in fisheries and loss of nursery habitats to coastal development, coupled with low reproductive potential have seen the population decline to less than 5% of its original size (Simpfendorfer 2002). Today, *P. pectinata* are found regularly only in the waters of southern Florida (Seitz & Poulakis 2002; Poulakis & Seitz 2004; Simpfendorfer & Wiley 2005). The population on the east coast of Florida was considered to have been extirpated (Snelson & Williams 1981), but is now known from a few recent records (Wiley unpublished data). In recognition of the extinction risk for the species, the National Marine Fisheries Service listed *P. pectinata* as Endangered under the US Endangered Species Act in 2003.

Despite the need for conservation of all sawfish populations, including *P. pectinata*, such efforts have been hampered due to the unsettled taxonomy of this group. The genus *Pristis* is taxonomically chaotic with uncertainty regarding the true number of valid species (Compagno & Cook 1995). The practical difficulties associated with resolving these taxonomic issues are acute, since it is extremely difficult to obtain specimens or tissue samples from these increasingly rare species for taxonomic research (Adams *et al.* 2006). Since the number of rostral teeth remains constant throughout the life of an individual (Slaughter & Springer 1968) rostral tooth counts have been employed as a potentially useful character by taxonomists studying Pristid systematics (Ishihara *et al.* 1991). To date rostral tooth count range reports have relied on museum specimens (often isolated rostra), counts from a small sample of animals, or of animals from a broad geographic range. This has resulted in uncertainty in the actual rostral tooth counts for each species. For example, published reports on the number of rostral teeth present on each side of the rostrum of *P. pectinata* vary considerably, including 24–32 (Jordan & Evermann 1896), 25–29 (Thorson 1973), 25–32 (Boschung 1979, Hoese & Moore 1998), 24–34 (Last & Stevens 1994) and 21–31 (Schwartz 2003). To clarify sawfish taxonomy, rostral tooth counts need to be better quantified for each species and for populations within species. This study reports a contemporary rostral tooth count distribution for the population of *P. pectinata* from the southeastern United States, and investigates the occurrence of sexual dimorphism and bilateral asymmetry in rostral tooth counts to aid in interpretation of rostral tooth count data.

Methods

Rostral tooth counts per side (left and right) and sex were recorded for 51 *P. pectinata* captured during directed sawfish research surveys conducted by Mote Marine Laboratory between 2001 and 2007 along Florida's southwest coast from greater Tampa Bay (28.2°N) to the outer Florida Keys (24.5°N) [see Wiley & Simpfendorfer (2007) for sampling methods]. In addition to examination of captured individuals, photographs containing a clear view of the rostrum, submitted by the public via sawfish encounter reports, provided 31 rostral tooth counts from sawfish caught by recreational and commercial fishermen between 2000 and 2006 from Florida (n=30) and Georgia (n=1) [see Simpfendorfer & Wiley (2005) for collection techniques]. As the sex of these individuals was unknown these data were not used in examinations of sexual dimorphism. Rostral tooth counts per side from 23 specimens collected from Florida waters between 1834 and 2000 and currently deposited in public or private collections were also taken. Collection specimens were directly examined to obtain rostral tooth count data and additional photographs and rostral tooth counts were supplied by collaborators (see *Collection material examined* below). In all cases, tooth counts represent tooth alveoli, and evident missing rostral teeth were included when determining rostral tooth counts.

The range and mean of rostral tooth counts (left, right and total) were calculated for groups –male, female, and all samples combined. The range and mean of rostral teeth per side, regardless of whether left or right, was also calculated. The significance of differences between the mean number of teeth on either side of the rostrum was calculated for males, females and combined sex data with a matched pairs t-test using JMP 5.1 (SAS Institute). Differences in the mean number of total, left and right rostral teeth between groups was tested with two-sample t-tests using JMP to determine if sexual dimorphism existed. Analyses were performed assuming equal variance after verifying that per side variance did not differ significantly (Bartlett test p value = 0.6807 and 0.6272 for right and left counts, respectively). Bilateral symmetry was assessed by determining the differences in counts between left and right sides for each rostrum. The frequency and direction of asymmetry was calculated and assessed using three tests. First, a chi-squared test was utilized to determine if the proportion of rostra with asymmetry was equal to the number with symmetry. Second, a chi-squared test was used to determine if the proportion of rostra with higher left tooth counts was equal to the proportion with higher right tooth counts. Third, a chi-squared goodness of fit test was applied to a Poisson distribution to determine if the frequency of differences matched a random distribution.

Collection material examined

P. pectinata from Florida, USA: AMNH 55558, isolated rostrum, 1834, Key West; BMNH 1906.8.14.47, juvenile male (662 mm TL), no specific locality; MCZ 89872, isolated rostrum, 2/1918, Key West, Monroe County; MCZ 153666, isolated rostrum, 1859 or earlier, stated “prob. Florida”, no specific locality; MCZ 153667, isolated rostrum, 1859 or earlier, stated “prob. Florida”, no specific locality; MR 0007 (M. McDavitt pers. col.), isolated rostrum, 1997 or earlier, no specific locality; UF 48061 (Z5677), isolated rostrum, 1960, Gulf of Mexico, Apalachicola Bay, Manatee County; USNM 00030678, juvenile male (675 mm TL), 1882, Gulf of Mexico, Pensacola; USNM 00110149, isolated rostrum, no specific locality; USNM 00205192, juvenile male (1,152 mm TL), Cocoa; YPM 8625, juvenile male (829 mm TL), 1886, Indian River, Brevard County. *Supplementary images or data*: LACM 39297.002 (F389 7060), image of isolated rostrum, no specific locality; LACM 39297.003 (F390), image of isolated rostrum, no specific locality; LACM 39297.004 (F392 A2826), image of isolated rostrum, no specific locality; LACM 39297.005 (F393), image of isolated rostrum, no specific locality; LACM 39297.006 (F394 A1317), image of isolated rostrum, no specific locality; LACM 39297.008 (F385), image of isolated rostrum, no specific locality; LACM 39297.009 (F387), image of isolated rostrum, no specific locality; LACM 42016.001 (F386), image of isolated rostrum from an adult (4,430 mm TL), 3/8/1882, Indian River Inlet; SU 10630, rostrum data from a juvenile male (690 mm TL), Gulf of Mexico; SU 14334, rostrum data from a juvenile male (750 mm TL), 5/1935, Tarpon Bay, Sanibel Island, Lee County; Uncat J. Seitz pers. col., image of isolated rostrum, 1940–1950, Gulf of Mexico, Collier County; Uncat J. Seitz pers. col., image of isolated rostrum, 2000 or earlier, no specific locality.

Results

Distribution of rostral tooth counts. Total rostral tooth counts ranged from 45 to 56 (mean 50.8) for the 105 specimens examined (Fig. 1). The count per side, irrespective of whether left or right, ranged from 22 to 29 (mean 25.4). Counts of left side rostral teeth varied between 23 and 28 (mean 25.3), while right side counts had a slightly greater range varying from 22 to 29 (mean 25.2) (Fig. 2A). Although the ranges differed between sides there was no significant difference in the means (matched pairs t-test, $t = 1.104$, d.f. = 104, $p = 0.272$).

Gender information was available for 51 specimens, 25 males and 26 females. Males left rostral tooth counts ranged from 24 to 28 (mean 25.9) and right counts from 23 to 28 (mean 25.8) (Figure 2B), and there was no significant difference in the mean counts between sides for males (matched pairs t-test, $t = -0.161$, d.f. = 24, $p = 0.873$). Female left side rostral tooth counts ranged from 23 to 28 (mean 25.1) and right side counts ranged from 22 to 28 (mean 25.3) (Figure 2C). There was no significant difference in the mean counts between sides for females (matched pairs t-test, $t = 0.775$, d.f. = 25, $p = 0.446$).

Sexual dimorphism. As shown above, males had higher mean values for both left and right rostral tooth counts when compared to females. The mean number of rostral teeth on the left side was significantly higher for males than females (t-test, $t = -2.580$, d.f. = 49, $p = 0.013$), but the mean number of rostral teeth on the right side did not significantly differ between the sexes (t-test, $t = -1.653$, d.f. = 49, $p = 0.105$). Mean total rostral tooth counts were also significantly greater for males than females (t-test, $t = -2.472$, d.f. = 49, $p = 0.017$).

Bilateral asymmetry. Bilateral asymmetry occurred in 77 out of 105 specimens (73.3%), with differences between left and right sides ranging from zero to three (Fig. 3). The proportion of individuals that displayed asymmetry was significantly greater than those that did not (Chi squared test, $\chi^2 = 22.88$, d.f. = 1, $p < 0.0001$). For those individuals with asymmetry, the proportion with left dominant counts was not significantly different to those with right dominant counts (Chi squared test, $\chi^2 = 1.58$, d.f. = 1, $p = 0.208$). The frequency of differences in tooth counts between left and right sides did not conform to a Poisson distribution (Chi squared test, $\chi^2 = 19.25$, d.f. = 2, $p < 0.0001$) indicating that differences were not the result of a random process.

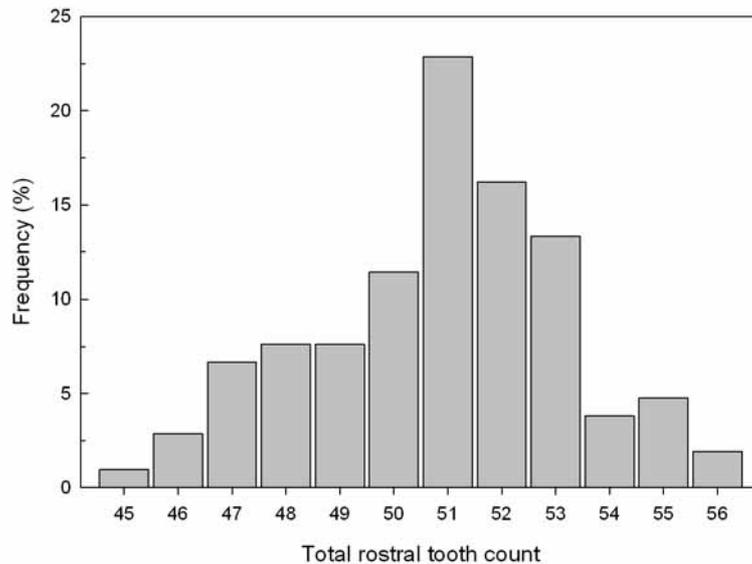


FIGURE 1. Relative frequency of total rostral tooth counts for *Pristis pectinata* from the southeastern United States (n=105).

Discussion

Rostral tooth count range. The observed rostral tooth count range for *P. pectinata* from the current study (22–29 per side) is different from previously reported counts for *P. pectinata*. In most cases, previous authors have reported maximum counts above 31 and minimums of 24 or 25 (Jordan & Evermann 1896; Bigelow & Schroeder 1953; Thorson 1976; Last & Stevens 1994; Schwartz 2003). Compagno and Last (1999) provide a range of 20–32 and usually 25–29 pairs. There are at least three possible reasons why the observed rostral tooth counts differed from previously reported values. The first likely reason for a difference between the rostral tooth count range obtained in this study and previously reported values is that misidentification and taxonomic uncertainty lead to historic misidentification of specimens (Thorson 1976; Zorzi 1995; Eschmeyer 1998; Martin 2005). Thus previously published rostral tooth counts potentially included data from other species. This type of error is even more likely to occur when counts were taken from isolated rostra. *Pristis pectinata* was long believed to have a circumglobal distribution in most warm-temperate to tropical continental inshore seas, and in lakes and rivers (Last & Stevens 1994, Compagno & Last 1999). However, reports of this species outside of the Atlantic are now considered to have been misidentifications of other *Pristis* species (Simpfendorfer 2005, Adams *et al.* 2006). Misidentification of *P. clavata* Garman as *P. pectinata* may have been responsible for exceptionally low reported rostral tooth counts for *P. pectinata*. Misidentification of *P. zijsron* Bleeker as *P. pectinata* may have inflated the maximum limit of the reported rostral tooth count range for *P. pectinata*. Since rostral tooth counts have historically been used to identify sawfish, this artificially broad rostral tooth count range for *P. pectinata* could have lead to a circular process of misidentification. For example, Schwartz (2003) erroneously included one *P. zijsron* specimen (USNM 263284) in his study of *P. pectinata*.

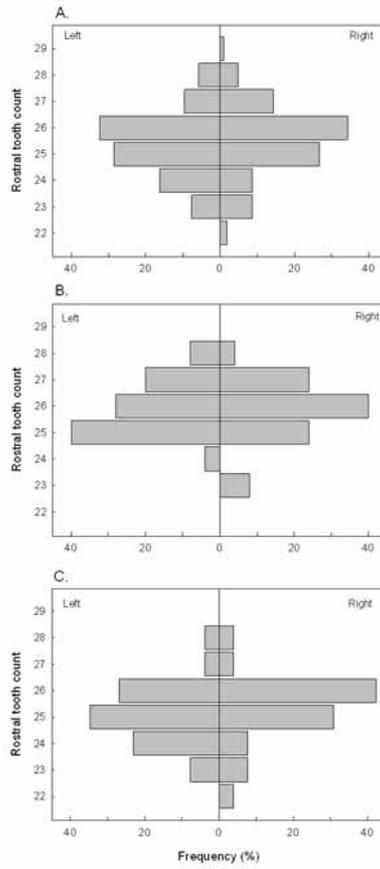


FIGURE 2. Relative frequency of left and right side rostral tooth counts for *Pristis pectinata* specimens from the southeastern United States. A) All specimens (n= 105). B) Males (n=25). C) Females (n=26).

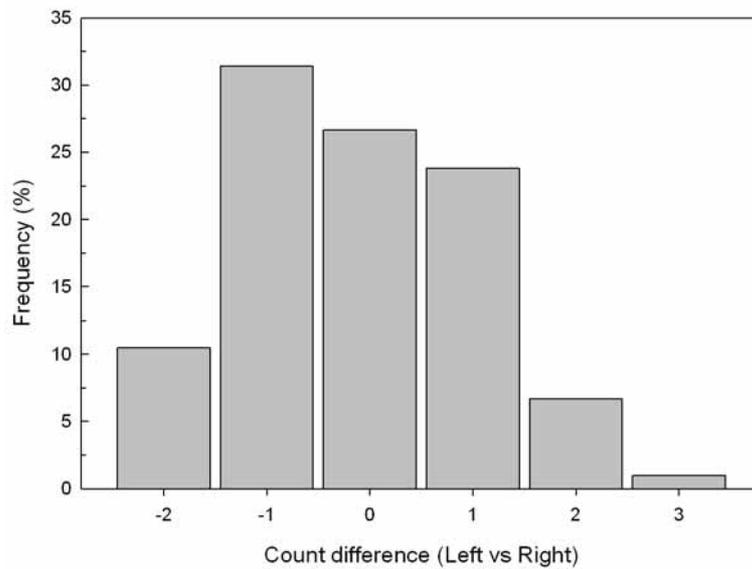


FIGURE 3. Relative frequency of rostral tooth count bilateral asymmetry in *Pristis pectinata* from the southeastern United States (n=105)

The second likely explanation is that inconsistent methodology has previously been employed in counting and reporting rostral tooth count data. For example, some sources identify the number of rostral teeth as the number of “pairs” of rostral teeth (McEachran & Fechhelm 1998, Cervigón & Alcalá 1999, Compagno & Last 1999, Simpfendorfer 2005), though *P. pectinata* most often exhibits unequal side rostral tooth counts. Hoese and Moore (1998) report “25–32 rostral teeth” not clarifying per side. Missing rostral teeth can result in under-estimates of rostral tooth counts if not correctly accounted for. In this situation, the alveolus or scar should still be counted to obtain accurate counts. Similarly, inaccuracies in rostral tooth counts can occur when viewing isolated rostra, such as those in museum or personal collections, if care is not taken to ensure that the rostrum is whole and all rostral teeth are present. If the rostrum was cut or broken between rostral teeth the rostrum would exhibit an artificially lower rostral tooth count. In most cases these methodological issues would have resulted in under-estimates of counts, and thus do not account for the lower maximum counts observed in the current study. These methodological inconsistencies may have occurred in previous studies, but it is difficult to ascertain the existence of errors in the rostral tooth count ranges in the literature. Therefore, the present study of the rostral tooth count range for *P. pectinata* was based primarily on live or collected specimens from the same locality under standardized count techniques.

A third potential cause for the lower rostral tooth count range obtained in this study (22–29 per side) in comparison to literature may be geographic variation in rostral tooth counts. Nevertheless, rostral tooth count data recently available for W. African *P. pectinata* (Robillard and Séret, 2006) asserts for a even lower count range (20–25, n= 15; a rostrum with 17 counts per side is likely an artifact and must be disregarded). Therefore, based on the limited information available, geographical variation within the Atlantic may not be a source of higher count values. Ishihara *et al.* (1991) reported that there was no significant difference in rostral tooth counts for *P. microdon* Latham between four geographic areas in northern Australia and Papua New Guinea. As noted by Hubbs and Hubbs (1945), in order to be able to account for possible geographic variation in rostral tooth counts, a large series of counts per locality are needed. Therefore, the full nature of sawfish rostral tooth geographical variation remains to be explored. Further investigation on this subject is currently under way.

Sexual dimorphism in rostral tooth counts. The results of this study indicate *P. pectinata* exhibit sexual dimorphism of rostral tooth counts. Thorson (1973) attempted, but was unable, to conclude from only three male and three female specimens that *P. pectinata* exhibited sexual dimorphism. However, significant sexual dimorphism has been reported in other species of *Pristis*. Thorburn *et al.* (2007) found that both the number of left rostral teeth and the total number of rostral teeth of male and female *P. microdon* in Western Australia were significantly different, with females possessing fewer rostral teeth than males. Ishihara *et al.* (1991) also reported that rostral tooth counts were significantly different between sexes of *P. microdon*, with males averaging 2.0 more rostral teeth per side than females. Thorson (1973) found that in Central America, *P. perotteti* Müller & Henle males averaged 2.1 more rostral teeth per side than females. Thorson (1973) also observed that in 25 out of 28 *P. perotteti* litters, all males possessed higher rostral tooth counts than all females; in only three litters did the highest female total count equal the lowest male count, and in no litters did a female count exceed any male count. Sexual dimorphism in rostral tooth counts therefore appears to be a consistent feature of the “largetooth group” within the genus *Pristis* (i.e. *P. microdon* and *P. perotteti*). The current study is the first confirmation of sexual dimorphism within the “smalltooth group” (*P. clavata*, *P. pectinata* and *P. zijsron*). The amount of difference between counts for male and female *P. pectinata*, however, was less than for that reported for *P. microdon* and *P. perotteti*. The collection of data from other species and other regions may help understand the full extent of sexual dimorphism in rostral tooth counts within the Pristidae.

Sexual dimorphism in elasmobranchs has mostly been reported in terms of size (i.e. females normally grow larger than males of a species). However, some species (especially rays) display sexual heterodonty of oral teeth (McEachran 1977) with male teeth functioning in both feeding and mating, and female teeth functioning only in feeding (Kajiura & Tricas 1996). Variability of the morphometric dimensions of skates with

size and between sexes has been reported (Braccini & Chiaramonte 2002, McEachran 1982) and several species of skates often differ in the relative size of many parts of the head (Hubbs & Ishiyama 1968). Many evolutionary and ecological forces can be responsible for sexual dimorphism. Casselmann & Schulte-Hostedde (2004) reported that differences in the selective pressures experienced by the sexes could result in the evolution of sexual dimorphism of morphological traits. However, the selective forces that have acted on sawfish to produce sexually dimorphic rostral tooth counts are currently unclear and further research is necessary to determine the mechanisms shaping the sexual dimorphism in *P. pectinata* rostral tooth counts.

Rostral tooth count bilateral asymmetry. The results of this study indicate that there was no significant difference between the left and right side rostral tooth counts when the population was considered. However, most individuals displayed bilateral asymmetry in the number of rostral teeth. The frequency of occurrence of asymmetry was greater than reported for other species of sawfish. For *P. microdon* in Western Australia, Thorburn *et al.* (2007) reported that 63% of females and 44% of males had the same number of rostral teeth on both the left and right sides of the rostrum, and also found that the asymmetry was not statistically significant at the population level. Ishihara *et al.* (1991) reported the greatest difference between sides of an individual was two more rostral teeth on the left side, with 48.8% of the rostra having equal numbers of rostral teeth on both sides for *P. microdon*. Thorson (1973) reported for *P. perotteti* the greatest difference between sides was three more rostral teeth on one side, with 56.4% of the rostra having equal numbers, and also found that the asymmetry was not statistically significant. The occurrence of bilateral asymmetry in rostral tooth counts of *P. pectinata* (73.3%) was much higher than for these other two species, which are more closely related to each other. Further research is required to determine the function and cause of the bilateral asymmetry in rostral tooth counts of sawfish. In particular, the non-random distribution of rostral tooth count differences needs to be further investigated. Current genetic studies may determine if the population has lost genetic variability, a possible cause of asymmetry.

Concluding remarks. This study has provided accurate rostral tooth count data for the *P. pectinata* population in the southeastern United States. This demonstrates the need to obtain contemporary data from other parts of this species' range, and from other *Pristis* species, to help in resolving taxonomic and distributional issues related to this genus. Such resolution will provide for more effective conservation planning for one of the most threatened groups of elasmobranchs. However, the rarity of sawfish in many parts of the world will also make it more difficult to obtain current data, and in some instances accurately identified material from collections may be needed to help provide these data.

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