

Mating scars reveal mate size in immature female blue shark *Prionace glauca*

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The objective of this study was to determine the size and maturity status of the male blue sharks *Prionace glauca* attempting to mate with small, immature females in the north-west Atlantic Ocean. The relationship between male curved fork length (L_{FC}) and jaw gape was used in conjunction with the diameter of the mating scar to estimate the L_{FC} and infer the maturity status of the male shark that produced the mating scar. The results indicate that mature males with a mean \pm s.d. L_{FC} of 218 cm \pm 23 cm were attempting to mate with sexually immature females.

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The blue shark *Prionace glauca* (L. 1758) is a large pelagic carcharhinid with a circumglobal distribution throughout tropical and temperate oceans (Compagno, 1984). Despite their wide distribution, *P. glauca* have never been directly observed mating so little is known about their reproductive behaviours (Litvinov & Laptikhovsky, 2005). Current information on *P. glauca* reproduction comes primarily from dissection (Pratt, 1979), tagging studies (Casey & Kohler, 1991) and inferred behaviours based on direct observations of other large shark species (Tricas & Lefevre, 1985). While some aspects of *P. glauca* reproduction, such as the timing and location of mating, can be determined through dissection and tagging studies, alternate approaches are required to help understand precopulatory behaviour and the size at which mating begins, topics that are important for understanding population structure.

Prionace glauca in the North Atlantic Ocean form a breeding population that extends from the east coast of North America to the west coast of Europe (Casey & Kohler, 1991). Mating occurs between late May and early November and pupping is believed to occur c. 9–12 months after insemination (Kohler *et al.*, 2002). In the north-west Atlantic Ocean, the *P. glauca* population is primarily composed of sexually immature

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males and females, and sexually mature males (Casey, 1985; Nakano & Stevens, 2008). Despite the fact that very few of the females in the north-west Atlantic Ocean are sexually mature, the presence of fresh spermatozoa in the oviducal glands of some of the immature females, along with fresh bite marks on their bodies, suggests that some of these sexually immature females are mating (Pratt, 1979; Pratt & Carrier, 2001).

Among elasmobranchs, it is common for males to bite females as part of a precopulatory ritual; this behaviour is referred to as precopulatory biting (Pratt & Carrier, 2001). When sharks engage in precopulatory biting, the male will either bite the female on the anterior end of her body (commonly between her gills and first dorsal fin) or on her pectoral fins (Stevens, 1974; Wourms, 1977; Pratt, 1979; Tricas & Lefevre, 1985; Pratt & Carrier, 2001; McCauley *et al.*, 2010). These scars appear as semi-circular jaw impressions and individual tooth cuts and are referred to as either mating or courtship scars (Springer, 1967; Stevens, 1974). Males have not been recorded with scars resembling mating scars, suggesting that females do not reciprocate this behaviour (Springer, 1967; Pratt, 1979; Tricas & Lefevre, 1985).

Despite the widespread distribution of immature females with mating scars in the north-west Atlantic Ocean (Pratt, 1979), the size and maturity status of the males attempting to mate with these immature females remain unknown. The objective of this study was to determine if mating behaviour is limited to sexually mature males, or if both mature and immature males attempt to mate with immature females. By measuring the bite diameter of mating scars on immature female *P. glauca*, the hypothesis that sexually immature males attempt to mate with immature females was tested.

Prionace glauca were measured during the summer months (July to August) at 82 shark fishing tournaments held throughout Nova Scotia, Canada, from 1993 to 2011. All fish were caught using rod and reel. Since this study focused on immature females, sexually mature females (which were rare) were excluded from analysis, leaving measurements of 754 mature and immature males and 24 immature females.

The fork length (L_F) of each fish was measured over the body curve (L_{FC} ; see Campana *et al.*, 2004 for morphometric conversion formulas). The lateral jaw gape of each male shark (the width of the jaw from the outer tooth edge of the left posterior jaw angle to the right posterior jaw angle) was measured in a straight line. When immature female fish with mating scars were landed, the number and diameter of the mating scars (identified as distinct, semi-circular bite marks) were recorded. Mating scars that appeared incomplete (*i.e.* individual tooth marks) were not recorded, as an incomplete scar could not be used to estimate the lateral jaw gape of the male that inflicted the bite. Although only mating scars that appeared to be complete (*i.e.* showing a complete arc) were recorded, it is possible that some scars were not complete, which would mean that some males may have been larger than was estimated from their scars.

Males were considered sexually mature if their claspers were heavily calcified and could be rotated freely, if their rhipidion could be opened and the terminal hook extruded, and if dissection of the epididymis revealed the presence of sperm ($n = 611$). Males without these traits were classified as immature ($n = 143$). Female sexual maturity was assessed by inspecting the ova and uterus. Females with an enlarged uterus and ova >16 mm in diameter were considered sexually mature (Pratt, 1979). A small uterus and a lack of ova indicated an immature female, but only immature females with distinct mating scars were used in this analysis ($n = 24$). Two of the females included in this study had ova that were beginning to develop (*i.e.* were visible), but

were still very small, which suggested that the females were not completely sexually mature. Three ova diameter measurements were recorded for each of these females.

The L_{FC} of the biting male (the male that attempted to mate with the immature female) was estimated by using the mating-scar diameter as the independent variable in a length–gape model. To avoid pseudoreplication of the data, mean bite size was used when multiple bites were present on a single female. The sexual maturity status of the biting males was inferred based on their estimated L_{FC} relative to the length at which 50% of *P. glauca* males in the north-west Atlantic Ocean reach sexual maturity (L_{50}), which is 201 cm (Campana *et al.*, 2004).

The mean \pm S.D. L_{FC} of the immature female *P. glauca* with mating scars was 173 ± 9 cm, with a range from 162 to 201 cm. These values were unimodally distributed with a peak between 165 and 170 cm, with one individual >200 cm. Two of the immature females had ova diameters between 5 and 7 mm, which are too small to be considered sexually mature.

Male *P. glauca* were considerably larger than the females, with a mean \pm S.D. L_{FC} of 235 ± 35 cm. Generally, males with $L_{FC} < 200$ cm were sexually immature, whereas males with $L_{FC} > 200$ cm were sexually mature. There were 11 mature males, however, that had $L_{FC} < 200$ cm and 26 immature males that had $L_{FC} > 200$ cm.

Jaw gape increased non-linearly with the L_{FC} of male fish (Fig. 1). As the maturity status of the biting males was unknown, all males were included in the model to represent the entire range of the length–gape relationship that could be applied to the biting males. When the males of all maturity states were combined, an inverse model fit the data well ($P < 0.01$, $r^2 = 0.68$). There were distinct sub-groups of immature and mature males, however, within the male length–gape data (Fig. 1). A power model was not used due to poor residual distribution.

When mating-scar diameter was used as the independent variable in the inverse model, the mean \pm S.D. L_{FC} of the biting males was estimated to be 218 ± 23 cm (Fig. 2). The smallest male was estimated to have an L_{FC} of 180 cm and the largest male was estimated to have an L_{FC} of 260 cm.

There was no significant relationship between the estimated L_{FC} of the male and that of the immature female with which it was trying to mate ($P > 0.05$). The L_{FC} range of the immature females with mating scars, however, was relatively small, leaving open the possibility that there may have been a relationship if both immature and mature females had been examined.

The mating scars observed on sexually immature female *P. glauca* in the north-west Atlantic Ocean were probably caused by sexually mature males. In the north-west Atlantic Ocean, male *P. glauca* begin to mature when they reach an L_{FC} of 160 cm and are all effectively mature by 220 cm (Campana *et al.*, 2004). In this study, the mean \pm S.D. L_{FC} of the biting males was 218 ± 23 cm. Therefore, the males that attempted to mate with sexually immature females were most probably sexually mature. Based on this conclusion, the original hypothesis that immature males in the north-west Atlantic Ocean attempt to mate with immature females is rejected.

The length–gape relationship in male *P. glauca* in the north-west Atlantic Ocean changes as the fish mature. Immature males have a proportionately smaller body length and wider jaw gape compared with mature males. The observation that the relationship between L_{FC} and jaw gape varies depending on maturity status has not been previously shown in a large shark species, but a similar finding was observed with the Port Jackson shark *Heterodontus portusjacksoni* (Meyer 1793). Powter *et al.* (2010) proposed that

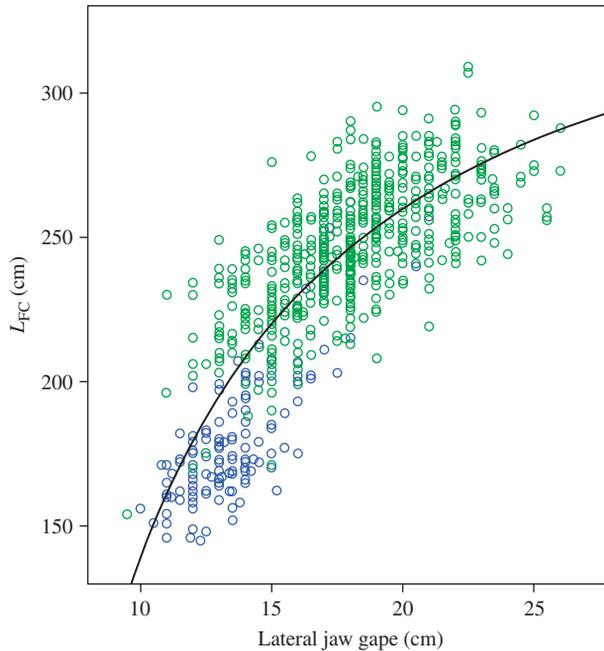


FIG. 1. The relationship between curved fork length (L_{FC}) and lateral jaw gape for immature (\circ) and mature male (\odot) *Prionace glauca*. An inverse model has been fit to the data following the equation: $y = 379.46 + (-2397.18)x^{-1}$.

the mouths of sub-adult *H. portusjacksoni* may grow at a faster rate than their bodies as an energy trade-off between overall body growth *v.* sexual maturation and the development of adult dentition (to allow for access to a broader diet). Although this hypothesis may or may not apply to *P. glauca*, the dentition of male *P. glauca* does change from knife to fork-shaped as males mature, which is presumably beneficial to the females as it helps the males hold the females during copulation instead of slicing them (Litvinov & Laptikhovskiy, 2005).

In this study, the mean \pm s.d. L_{FC} of the females with mating scars was 173 ± 9 cm, with a range from 162 to 201 cm. To compare these results with those of Pratt (1979), Pratt's straight fork length (L_{FS}) measurements have been converted to L_{FC} measurements using a formula from Campana *et al.* (2004; $L_{FC} = 2.1 + 1.0 L_{FS}$). Altogether, these results suggest that in the north-west Atlantic Ocean, some male *P. glauca* begin mating with females once the females have L_{FC} between 147 and 173 cm, although some males may attempt to mate with females as small as 136 cm. Pratt (1979) also reported, however, that in north-west Atlantic Ocean *P. glauca* females begin to sexually mature when they reach an L_{FC} of 187 cm. Thus, in the north-west Atlantic Ocean, male *P. glauca* appear to be mating with sexually immature females.

While the females with mating scars examined in this study were sexually immature, according to Pratt (1979), some could be re-categorized as sub-adult. To explain why males attempt to mate with small females, Pratt proposed that female *P. glauca* develop through three maturity stages: immature, sub-adult and mature. He proposed that sub-adult females are between 145 and 185 cm with partially developed generative

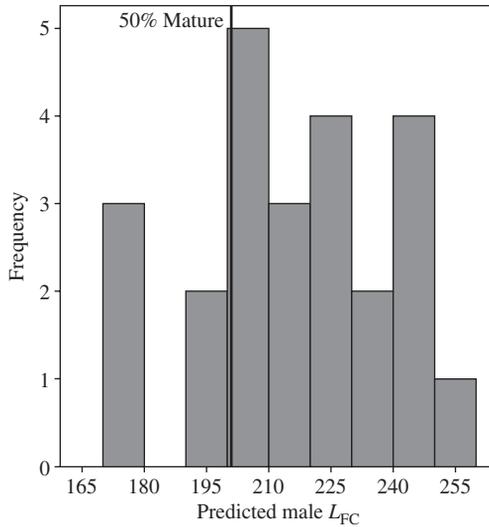


FIG. 2. The estimated curved fork length (L_{FC}) of the male *Prionace glauca* that attempted to mate with sexually immature female *P. glauca* ($n = 24$, mean \pm s.d. = 218 ± 23 cm), based on an inverse L_{FC} -gape model that incorporated all of the males in this study. —, the L_{FC} at which 50% of male *P. glauca* in the north-west Atlantic Ocean reach sexual maturity (201 cm; Campana *et al.*, 2004).

organs (*i.e.* mature females have ova > 16 mm in diameter while the ova of sub-adults are between 2 and 6 mm). While 22 (92%) of the females observed in this study fell within the sub-adult length range, only two of the 22 (9%) had visible ova (between 5 and 7 mm) and therefore could qualify as sub-adult based on Pratt's description. Further morphological research is required to confirm that a sub-adult female is a valid maturity status (Castro, 2011).

It was not always possible to confirm that the mating scars measured in this study were complete jaw impressions. If a bite impression was incomplete, it would result in the estimated length of the biting male being underestimated. Thus, any measurement bias in the study would serve to reinforce the conclusion that mature males, not smaller immature males, were attempting to mate with immature females.

There was no significant relationship between the estimated L_{FC} of the biting male and that of the female with which it attempted to mate. This finding is consistent with the fact that *P. glauca* are generally segregated by sex and maturity status (Stevens, 1990), except during the mating season. When males and females meet during the mating season, the males attempt to mate with as many females as possible. Additionally, sexually mature females are very rare in the north-west Atlantic Ocean (Campana *et al.*, 2004) and it is possible that the mature males present in these waters adapt to this by mating with any female that appears large enough to be mature. Males may recognize that some females are too small and insufficiently developed to mate with, hence the lack of mating scars on very small females (Pratt, 1979).

Shark length-gape relationships have been used to answer a range of research questions. The results of this study, however, suggest that the accuracy of the predictions made with length-gape relationships could be improved if researchers can first determine if the relationship changes with the maturity status of the species in question. In

this study, if the maturity status of the biting males was known there would have been less variation in the range of their estimated L_{FC} .

The conflicting results from this study and that of Pratt (1979) in terms of determining the maturity status of female *P. glauca* indicate that even with dissection, determining the maturity status of these females can be complicated. The uncertainty regarding whether or not to categorize females as sub-adults should be investigated further as the result may have implications for the understanding of *P. glauca* reproduction in the Atlantic Ocean. If the term sub-adult is shown to be a valid maturity status, and if sub-adult females are capable of storing sperm and delayed fertilization, it would be important to know where these sub-adults are mating and if this comprises a major part of the mating population.

The current understanding of *P. glauca* population structure in the north-west Atlantic Ocean indicates that *P. glauca* mating occurs throughout the North Atlantic Ocean (Pratt, 1979; Campana *et al.*, 2004; Mejuto & García-Cortés, 2005; Nakano & Stevens, 2008). Similarly, pupping areas are believed to be located in the eastern and central North Atlantic Ocean (Stevens, 1976; Vandeperre *et al.*, 2014). Given that sexually mature males appear to be copulating (based on the presence of mating scars) with immature females in the north-west Atlantic Ocean, it is conceivable that females inseminated in the north-west Atlantic Ocean and then migrate across the Atlantic to give birth in the pupping grounds in the north-east. These migrations could be more complex with females migrating to the tropical Atlantic prior to entering the eastern North Atlantic (Vandeperre *et al.*, 2014). The concept of mating in one area and then migrating to give birth in another has been previously proposed with the porbeagle *Lamna nasus* (Bonnaterre 1788) (Campana *et al.*, 2010), although the evolutionary significance of these migrations remains unknown.

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