Group courtship, mating behaviour and siphon sac function in the whitetip reef shark, *Triaenodon obesus*

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We analysed video records of three mating events involving nine free-living whitetip reef sharks in Cocos Islands, Costa Rica to examine reproductive behaviour in this species. We describe several behaviours never before documented in this species, and four behaviours never before documented in any elasmobranch. Here, we also present the first hypothesis for the function of the male's paired reproductive organs, the siphon sacs, to be based on observations of mating sharks. We introduce terminology for three separate siphon sac structural components that are externally visible during courtship and mating in this species. Based on our analyses, as well as evidence from past mating studies, the siphon sacs in whitetip reef sharks appear to be used to propel sperm into the female's reproductive tract, not for flushing the female's reproductive tract of sperm from previous males. We discuss the implications of 'group courtship', 'siphon isthmus constriction', 'reverse thrusting', 'postrelease gaping' and 'noncopulatory ejaculation'.

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Understanding elasmobranch reproductive dynamics is critical to ensure proper management and conservation of this vulnerable group. Whereas much is known about other aspects of elasmobranch reproduction (Wourms 1977, 1981; Dodd 1983; Gilmore 1993), shark reproductive behaviour is poorly understood because of the difficulties of observing natural behaviour in free-living sharks and the artificial nature of studies in captive facilities. Because of these challenges, most aspects of shark reproductive behaviour have been inferred from dissections (e.g. Gilbert & Heath 1972; Pratt 1979; Gilmore et al. 1983; Castro 1996). Although recent observational studies (reviewed by Pratt & Carrier 2001) have enhanced our understanding of shark mating behaviour, most have been based on observations of captive animals (e.g. Castro et al. 1988; Uchida et al. 1990; Gordon 1993), or analyses of still photos from brief encounters with mating sharks (e.g. Johnson & Nelson

1978; Tricas & LeFeuvre 1985; Harvey-Clark et al. 1999). Only two studies, Carrier et al. (1994) and Pratt & Carrier (2001), have described mating based on video analyses of multiple mating events in free-living sharks.

This study is based on video analysis of three mating events in free-living whitetip reef sharks and provides new insight into shark reproductive behaviour and the functional mechanics of the siphon sacs. The siphon sacs are subdermal organs of the male reproductive system that are apparently only used, and externally visible, during mating. This makes them particularly difficult to study in dead or noncourting specimens.

Siphon sacs are paired, ventral organs associated with the claspers, and each siphon sac (right or left) ends blindly at its anterior end, and at its posterior end connects to an opening at the proximal end of the clasper called the apopyle. The clasper tube itself runs posteriorly from the apopyle to its distal opening called the hypopyle. When not mating, both the apopyle and hypopyle are posterior of, and have no connection to, the urogenital papilla, which is the terminus of the reproductive tract and site of sperm release just inside the cloacal opening. Although the siphon sacs have no direct connection to the urogenital papilla, most male sharks appear to rotate one clasper forward, forming a connection between the clasper apopyle and the urogenital papilla during mating. This rotation was first hypothesized by Leigh-Sharpe

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(1920) and has been supported by most observations of mating elasmobranchs (reviewed by Pratt & Carrier 2001).

After failing to find spermatozoa in any of the siphons of hundreds of specimens, Leigh-Sharpe (1920) proposed the currently accepted hypothesis that the siphons serve mainly as sea water reservoirs. While Leigh-Sharpe, and more recently Gilbert & Heath (1972), proposed that this sea water store served to propel sperm through the claspers, Eberhard (1985) suggested that the siphons might serve to flush the female reproductive tract of sperm from previous males before the copulating male injects his own sperm. Resolution of this debate, and elucidation of how either of these processes might work, has been hampered largely by a lack of behavioural observations of mating sharks.

In this analysis of courtship, mating behaviour and siphon sac functional morphology in free-living whitetip reef sharks, we provide the first documentation of several mating behaviours for this species, as well as four new behaviours that have not been previously described in any elasmobranch. We also describe newly observed morphological divisions of the siphon sacs and present a revised hypothesis regarding their functional mechanics. This is the first hypothesis of siphon sac function to be based on the in situ appearance of the naturally functioning siphon sacs.

METHODS

Digital video taken by S. Waterman at Cocos Island, Costa Rica in February 2001 recorded three mating events between whitetip reef sharks. There appeared to be hundreds of whitetip reef sharks present during 4 days of diving in the area, and the average water temperature was 24°C. Water depths at the site of mating activity varied from 12 to 18 m and reproductively active whitetips have been seen in this place and season for many years. From the video, it appeared that there were more males involved in the mating activity than females. We could not discern whether other females were nearby. Each mating event was attended by two or more males of a similar size to the engaged male(s) and with visibly mature claspers. These males often circled and passed the mating pair continuously at close range, usually less than a body length away. During the daylight diving operations, the whitetip reef sharks at Cocos Island seemed most sexually active in the morning. Courting animals were not noticeably disturbed by the presence of divers, and no other shark species were seen during these mating observations.

We captured the video from the master tape on a PC through an IEEE 1394 (Firewire) interface using MotoDV and PhotoDV software by Digital Origin. We saved video clips of each of the three mating events as four QuickTime files. Because of its length, we captured event 2 in two sections. We did not edit or transform the video record in any way.

We recorded spot patterns and fin abnormalities for all animals to determine whether the same animals were being observed in multiple mating events. We transcribed all behaviours into a spreadsheet for classification based on the terminology described by Pratt & Carrier (2001). We also tracked the extent of siphon sac inflation for each of the four males over the three mating events to characterize siphon sac functional mechanics. We follow Carrier et al. (1994) and Pratt & Carrier (2001) in using 'mating event' as a term that includes courtship and precoupling behaviours that may or may not lead to and include copulation. For analytical purposes, we considered mating event duration to be the time from a male's initial grasp of a female pectoral fin until the time of fin release.

RESULTS

We determined actively courting individuals to be different in each of the three mating events based on their spot patterns and fin markings. Most surrounding males also appeared to be different for each event, although one male was observed circling during both events 1 and 2. Of the three mating events analysed, two (events 1 and 3) were between a single male and female per event. The other (event 2) initially involved four males and one female, with two of the males achieving pectoral fin grasps on the female. All events concluded on the substrate, although at least two were initiated in midwater, with the animals sinking to the bottom as a result of inhibited swimming during copulation or precopulatory manoeuvring. Only one of the three events (event 3) resulted in copulation.

Siphon Sac Morphology and Terminology

The siphon sacs of adult male whitetip reef sharks extend the length of the abdominal body wall from near the origin of the pectoral fins to the proximal surface of the pelvic fins. Each of the paired siphon sacs thus occupies approximately one-third the length of the body and is morphologically differentiated into three separate regions: the anterior sac, the siphon isthmus and the pelvic sac (Fig. 1). When fully inflated, the anterior sac

Figure 1. Three distinct regions of the left siphon sac are visible in male B during mating event 2: AS = anterior sac; SI = siphon isthmus; PS = pelvic sac. The siphon isthmus is constricted in this frame. Copyright S. Waterman. Used with permission.

Table 1. Extent of siphon sac inflation, mating event duration and outcome for each of four male whitetip reef sharks over three separate mating events

Mating event	Male	Anterior sac	Siphon isthmus	Pelvic sac	Duration (s)	Outcome of event
1	A	Inflated	Not visible	Not visible	>68	Separated without insertion/copulation Sperm discharged into water column
2	B	Inflated	Constricted	Dilated	>113	Unknown/no insertion observed
2	C	Inflated	Dilated	Dilated	80	Separated without insertion/copulation
3	D	Inflated	Dilated	Dilated	>151	Copulation

occupies nearly the entire width of the ventral abdominal surface and extends from the origin of the pectoral fins to a point below the insertion of the first dorsal fin. The siphon isthmus is a narrower, tubular region extending from the anterior sac to a point just anterior to the pelvic fin. The siphon isthmus can be either dilated or constricted (Fig. 1) while other siphon components are inflated. The pelvic sac is the region running along the medial, ventral surface of the pelvic fin from the siphon isthmus to the clasper. As in all elasmobranchs, each set of siphon sac components is paired and equally present on both sides of the ventral surface, with a patent connection to its respective clasper.

The extent of siphon sac inflation, event duration and outcome for males A through D are summarized in Table 1. Inflation of the anterior portion of the siphon sac was observed in each of the four males that successfully grasped the pectoral fin of a female, although the state of other siphon components differed between males and events. Only males B and C were visible prior to siphon sac inflation and neither showed inflation before first obtaining a pectoral grasp and rotating one clasper forward. The siphon sacs were never clearly visible during inflation.

Event 1: Female Avoidance and Noncopulatory Ejaculation

Video of event 1 begins with male A already grasping the right pectoral fin of a similarly sized female, and with his right clasper rotated forward and ready for insertion (Fig. 2). Male A showed full inflation of the right anterior sac, but the siphon isthmus and pelvic sac were obstructed from view by the body of the female for most of the event. The male grasped the pectoral fin of the female for over 68 s but was unable to achieve clasper insertion due to three female actions (Fig. 2). First, by continual manoeuvring, the female was able to maintain her ventral surface to the substrate, limiting access to her cloaca. In a second related activity, she rolled the distal half of her left pectoral fin under her body, keeping it away from other males while still providing leverage to maintain her upright position. Third, as male A thrust, she kept her tail tightly arched below his abdomen and curved against his clasper, thus preventing access to her cloaca and giving her body upright stability so she could not be overturned. All observed females repetitively opened their mouths to facilitate nonswimming respiration during mating activities.

Upon releasing the female's pectoral fin, the male's clasper immediately rotated caudally, back to its resting position, while the anterior sac remained inflated. Five seconds after releasing the female's pectoral fin, while swimming away, male A expelled a cloud of ejaculate that exited the body anterior to the clasper hypopyle, either from the clasper apopyle or from the urogenital papilla itself (Fig. 3). Male A departed this event swimming with his mouth agape, as did male C in event 2 (Fig. 4).

Event 2: Group Courtship

Event 2 began in midwater 5–10 m above the substrate. At the onset, four males simultaneously surrounded and made contact with one female in an attempt to grasp her pectoral fins. The first male (male B) successfully grasped the female's left pectoral fin while the three remaining males tried to grasp the female's right fin (Fig. 5). Once the female's right pectoral was grasped by a male (male C), the remaining males withdrew while the three engaged sharks (two males, one female) spiraled to the substrate. Each engaged male showed one rotated clasper and subsequent inflated siphon sac within seconds of grasping a pectoral fin, and both used repetitive caudal fin undulations to

Figure 2. A female whitetip reef shark (forefront) maintains her ventral surface to the substrate, rolls her left pectoral fin under her body to guard it from other males, and arches her tail to the side, preventing access to her cloaca during mating event 1. Male A has grasped the right pectoral fin of the female, and rotated his right clasper (arrow) forward for insertion. Copyright S. Waterman. Used with permission.

Figure 3. Male A (above) expels ejaculate into the water column 5 s after releasing his grasp on the female (below) during event 1. The ejaculate cloud begins anterior to the hypopyle, the opening at the distal end of the clasper. Copyright S. Waterman. Used with permission.

position themselves for copulation. Although male bites were obviously firm and controlling, the jaws of both males were open far enough to not only encompass the female's fins but to nearly meet each other at her ventral midline (Fig. 6). No gill pumping by males was observed during fin grasps in any of the three mating events.

Figure 4. Males A (top) and C (bottom, mouth circled) both depart failed copulation attempts with their mouths agape. Copyright S. Waterman. Used with permission.

Figure 5. Four male whitetip reef sharks attempting to engage one female during mating event 2. One of the males (male B) has successfully grasped the female's left pectoral fin while the other three males are attempting to grasp her right pectoral fin. Copyright S. Waterman. Used with permission.

The female was able to avoid copulation with the engaged males by maintaining a strongly arched tail for the duration of the event, thus keeping her cloaca out of the range of the male claspers. Male B showed inflation of all three right-side siphon components within 17 s after initiating the pectoral grasp in midwater. After reaching the substrate, approximately 39 s after grasping the female, the same male (male B) constricted his siphon isthmus, apparently isolating the anterior sac from the pelvic sac (Fig. 1). In the same event, male C showed full inflation of the anterior sac, siphon isthmus and pelvic sac. This condition remained static throughout the event, again without insertion or copulation, before male C released his pectoral grasp after holding for 80 s. No ejaculation was noted in the 2 s before male C left the video frame, swimming with his mouth fully agape (Fig. 4). Event 2 continued with male B grasping the female for at least another 33 s before the video sequence ended.

Figure 6. Males B (above) and C (below) have engulfed the female's left and right pectoral fins, respectively, almost touching their jaws together at her ventral midline during event 2. Copyright S. Waterman. Used with permission.
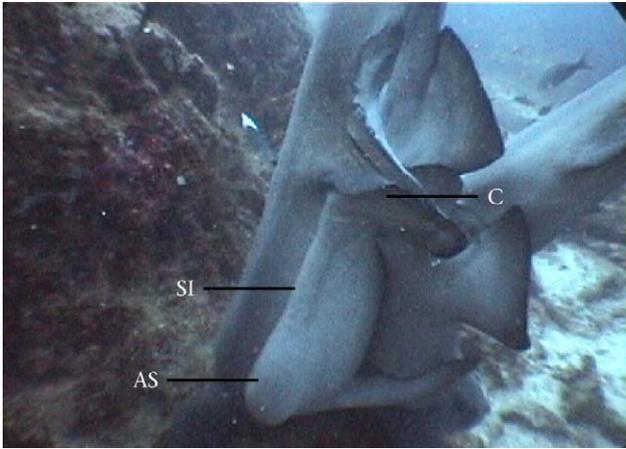
Figure 7. A copulating pair of whitetip reef sharks showing the left anterior siphon sac (AS), unconstricted siphon isthmus (SI), and inserted left clasper (C) of male D in event 3. Copyright S. Waterman. Used with permission.

Event 3: Copulation

Footage of the third mating event began with male D already grasping the female's left pectoral fin and achieving clasper insertion within 3 s of the start of filming. Siphon sac condition could not be determined until 8 s into the event, at which point all three siphon sac components were visibly inflated. The two sharks tumbled in copula down an underwater cliff face, with the male showing rapid caudal manoeuvring that brought the pair to rest in a vertical head-down orientation on a rocky wall. Once they came to this position, the male ceased his swimming movements and began rhythmic but variable thrusting of his pelvic region towards the female. They remained there for several seconds before falling and coming to rest twice more, each time maintaining parallel, head-down positioning (Fig. 7). The female did not arch her body to the side nor display any avoidance behaviours like those observed in events 1 and 2.

For most of the observed copulatory period, male pelvic thrusts were delivered at approximately 2-s intervals, with one or two short caudal undulations between each thrust. Thrusts consisted of both forward (towards the female) and reverse (away from the female) phases, which varied in forcefulness over the course of the event. Although the forward phase was the most forceful during the first 30 s of copulation, the reverse phase gradually became more forceful over the last 86 s during which the event was filmed. The clasper remained inserted in the female cloaca throughout the event.

At least four peripheral males with mature claspers circled the mating pair throughout the event. They nudged the female's free pectoral fin with their rostrums several times, but did not grasp it. Although male D was observed actively copulating for 151 s before filming ceased, all siphon components remained at least partially inflated (Fig. 7). At no point was the siphon isthmus of male D constricted, as was noted in male B (Fig. 1), although the anterior sac may have decreased slightly in size over the course of the event.

DISCUSSION

Behaviours observed in this study closely paralleled those catalogued by Pratt & Carrier (2001) from observations of mating in nurse sharks, Ginglymostoma cirratum, and other elasmobranchs. These behaviours include: 'arch', 'avoid', 'group behaviour', 'pectoral grasp', 'positioning and alignment', 'clasper flexion', 'insertion and copulation' and 'separating'. This is the first time several of these behaviours have been observed in whitetip reef sharks. Furthermore, the analysis of the video footage revealed additional mating behaviours that have not been previously observed in any elasmobranch. These include: 'siphon isthmus constriction', 'reverse thrusting', 'postrelease gaping', and 'noncopulatory ejaculation'. The implications of each of these behaviours are discussed below.

Female Avoidance and Mate Choice

'Avoidance' behaviours by females were noted in two cases (events 1 and 2) and consisted primarily of the female 'arching' her body to the side and keeping her cloaca out of reach after the male(s) had achieved a pectoral grasp. These avoidance behaviours are similar to those noted in female nurse sharks, which avoided copulation in 92% of the mating events observed by Pratt & Carrier (2001), and appear to be the basis of precopulatory mate choice. The cessation or absence of female avoidance behaviour in some mating events (event 3 of this study; Pratt & Carrier 2001) indicates that females may be cooperating with some males, and hence choosing them over others. While female sharks may often be unable to avoid male mating advances and pectoral grasps, they seem much more adept at avoiding clasper insertion and copulation. This is largely the result of the males' need to release their pectoral grasps after short periods, possibly due to oxygen deprivation (discussed below). This apparent female control of mate choice and copulation is consistent with sexual selection theory (Trivers 1972), although recent discoveries of multiple paternity within shark litters (Feldheim et al. 2001; Saville et al. 2002) indicate that postcopulatory factors are also an important part of sexual selection for some shark species.

Male Behaviour and Clasper Use

All four males initiated mating by attaining a 'pectoral grasp' on the female, rotating a clasper forward ('clasper flexion') and attempting to 'position and align' the female for copulation. Each male attempted to insert only one clasper and inflated only the siphon sac components associated with that clasper. The clasper (right or left) used by each male corresponded to the female pectoral fin (right or left) he had grasped. For example, a male would use the left clasper and siphon sac when the female's left pectoral fin had been grasped and she was thus on his right side. This is consistent with most previous observations of shark mating behaviour (reviewed by Pratt & Carrier 2001), and was first described as a pattern by Carrier et al. (1994). Clasper flexion across the cloaca

brings the clasper apopyle over the urogenital papilla (where sperm is released) and may form a necessary connection for sperm to pass through the clasper groove (Leigh-Sharpe 1920). Based on the origin of ejaculate release in male A (Fig. 3), and our unpublished observations of fresh material, it seems that sperm released from the urogenital papilla will not pass through the claspers if they are not rotated and flexed forward. Only male D achieved 'insertion and copulation' whereas males A and C were both observed 'separating' from females after failed attempts at copulation.

Group Courtship

Although group courtship behaviour has not been previously documented in whitetip reef sharks, this behaviour is common in nurse sharks (Carrier et al. 1994) and may be so in other species as well. The two males (B and C) that simultaneously grasped the same female in event 2 of this study appeared to be competing with each other rather than cooperating, because each displayed a rotated clasper and an inflated siphon sac. Although competitively motivated, group mating may be functionally cooperative if the probability of a given male achieving copulation increases when another male has also grasped the female. The presence of multiple males increased the probability of copulation in nurse sharks (Carrier et al. 1994), but neither male in event 2 of this study achieved clasper insertion during the 113-s filming of the event.

Although several studies have described aggregations that may be related to reproduction (e.g. Klimley 1985; McKibben & Nelson 1986; Economakis & Lobel 1998; Harvey-Clarke et al. 1999), we use the term 'group court-ship' here to refer to multiple males simultaneously grasping the same female. This behaviour has been observed in only two other elasmobranchs, the nurse shark (Carrier et al. 1994) and the southern stingray, *Dasyatis americana* (Chapman et al. 2003), and falls within the broader definition of 'group behaviour' as defined by Pratt & Carrier (2001).

Sperm Flushing or Sperm Propulsion?

Our analysis indicates that the siphon sacs of whitetip reef sharks serve to propel sperm into the female cloaca, not to flush the female reproductive tract of sperm from other males, as suggested by Eberhard (1985). There are several lines of evidence from this and previous studies that refute the sperm-flushing hypothesis.

First, the fact that the siphon sacs do not quickly deflate during copulation (Fig. 7) suggests that their main function is as a hydraulic pressure source forcing sperm through the clasper groove. Second, the physical presence of the clasper itself would inhibit the removal of sperm from the uterus; a male would have to remove his clasper at least once for sperm flushing and then reinsert to deposit his own sperm. Such is the case in organisms where the male intromittent organ is known to function in sperm removal (Waage 1979, 1986). Neither clasper

removal and reinsertion, nor sperm seepage from the female cloaca during copulation has ever been seen in this species (Tricas & LeFeuvre 1985; Uchida et al. 1990; this study) nor in any elasmobranch (reviewed by Pratt & Carrier 2001). Finally, males seem to have limited time in which to copulate once they have attained a pectoral grasp. These grasps commonly engulf the entire pectoral fin of the female and obstruct the mouth, and likely respiration, of the male (Fig. 6). The two males (A and C) observed to release their pectoral grasps swam away with their mouths agape in an apparent attempt to maximize water flow into the mouth and over the gills (Fig. 4). This 'postrelease gaping' indicates that males are deprived of oxygen during pectoral grasps, and this may limit mating event duration for whitetip reef sharks, as it appears to in the nurse shark (Carrier et al. 1994). Thus, given the fleeting and apparently oxygen-limited nature of shark copulation (no tests of blood oxygen done), taking the time to flush rival sperm from the female tract with sea water prior to insemination would probably diminish male reproductive fitness.

Siphon Sac Functional Mechanics: an Hypothesis

Male whitetip reef sharks initiate mating by grasping a female's pectoral fin, immediately rotating one clasper medially and forward, and inflating the siphon sac components associated with the rotated clasper. Upon inflation of the siphon sac, males are able to section off the anterior sac via 'siphon isthmus constriction' (Fig. 1). The main function of this may be to retain sea water in the anterior sac until copulation and/or to allow the pelvic sac to backfill with sperm from the urogenital papilla. During copulation, the siphon isthmus dilates (Fig. 7) and allows water from the anterior sac to propel sperm from either the pelvic sac or the urogenital papilla (via venturi force) through the clasper groove and into the female reproductive tract.

The robustness of the hypothesis described above and its application to other species can only be tested through further observations of mating sharks. In addition to several new findings presented here, our observations also raise questions regarding siphon sac functional mechanics.

Of the two males (B and C) whose siphon components were fully visible during precopulatory manoeuvring, male B constricted the siphon isthmus whereas male C did not (Table 1). From the extent of inflation shown by male C, it appears that complete constriction of the siphon isthmus is not required to maintain inflation of the anterior sac. More observations are needed to understand the timing and function of siphon isthmus constriction during precopulatory manoeuvring.

Questions remain about the lack of any extreme change in siphon sac condition during copulation (event 3). If the Leigh-Sharpe (1920) hypothesis that siphon sacs create the motive force for sperm transfer is correct, then one would expect more of a decrease in siphon sac volume to occur if filming had continued through to the conclusion of copulation. Footage of several copulations in nurse

sharks has also shown little change in siphon condition (H. L. Pratt & J. C. Carrier, unpublished data).

The condition of the siphon components of male A during ejaculation into the water column was not visible, although a rapid decrease in siphon volume would be expected in this instance. This futile ejaculation may indicate the backfill of sperm into the posterior siphon sac prior to clasper insertion. Given the presence of sphincter musculature around the urogenital papilla (H. L. Pratt, unpublished data), it would seem that a male should otherwise be able to retain sperm in the ampullae epididimides while evacuating sea water from the siphons after a failed mating attempt. However, the absence of sperm in the siphons of hundreds of specimens from several species (Leigh-Sharpe 1920; Gilbert & Heath 1972) contradicts the idea that sperm may enter the siphon sacs. Our observations do not shed light on the biochemical content of the ejaculate. Mann (1960) found large amounts of serotonin in the siphon sacs of spiny dogfish, *Squalus acanthias*, and proposed that this secretion may stimulate contractions in the male and/or female reproductive tracts.

Copulatory Position, Male Thrusting Behaviour and Siphon Sac Size

Upon achieving clasper insertion, male D 'positioned and aligned' the female into a parallel, head-down orientation on the substrate (Fig. 7). This copulatory position was identical to that described by Tricas & LeFeuvre (1985) in the only other study of mating in free-living whitetip reef sharks. One discrepancy is that Tricas & LeFeuvre noted that both of the male's siphon sacs were inflated in the single mating event they described. This is not apparent in the figures they present and seems doubtful in light of this and past studies on courting and mating sharks (reviewed by Pratt & Carrier 2001), which indicate inflation of only one (left or right) siphon sac at a time.

During copulation, male D maintained his pectoral grasp while repetitively thrusting his pelvic region. Thrusts were directed towards the female in the beginning of the event, with a brief withdrawal phase to prepare for each forward thrust. However, over the second half of the event, the withdrawal phase became more forceful than the forward phase and remained so until filming ceased. The purpose of this 'reverse thrusting' is unclear, but it may serve to maintain proximity to, or stimulate, the female during copulation. Stimulation of the female during copulation is not uncommon in the animal kingdom and may be further indication that postcopulatory factors are important in determining paternity of offspring (Eberhard 1990).

Relative siphon sac size can vary greatly between shark taxa (Gilbert & Heath 1972; Springer 1960) and this may be attributable to different mating systems. Whitetip reef sharks (this study) and other carcharinids (Springer 1960) have relatively large siphon sacs, whereas many ovoviviparous species appear to have relatively small siphon sac–body size ratios (Gilbert & Heath 1972). Variability in structures related to sperm transfer capability has been correlated to species' reproductive strategies in other animal groups (Harcourt et al. 1981; Eberhard 1985; Dixson 1987), but more data are needed for both mating strategies and siphon sac sizes before any such correlations can be made in elasmobranchs.

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