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A TEMPORAL, SEX-SPECIFIC OCCURRENCE PATTERN AMONG WHITE SHARKS AT THE SOUTH FARALLON ISLANDS, CALIFORNIA

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Based on 239 observations of 22 known-individual white sharks from 1987 to 2000, we report a temporal, sex-specific occurrence pattern among adult white sharks at the South Farallon Islands (SFI), California: individual males may occur every year, whereas individual females show a biennial occurrence pattern, being recorded every other year at most. This sex-specific occurrence pattern implies a 2-year reproductive cycle, resulting in a lower reproductive potential than previously thought, which has important implications for the conservation of this species. These results also suggest that female white sharks may travel significant distances in the North Pacific Ocean during a biennial reproductive cycle to give birth, whereas copulation may occur closer to northern California, allowing males to return annually to SFI.

INTRODUCTION

Segregation by sex has been reported for several species of sharks (Bigelow and Schroeder 1948, Bullis 1967, Pratt 1979, Gilmore 1993). Skewed sex ratios among capture data have indicated sex-specific aggregation patterns according to both geographic area and water depth. In the white shark (*Carcharodon carcharias*), spatiotemporal segregation by sex has been reported in North America (Casey and Pratt 1985, Klimley 1985), South Africa (Ferreira and Ferreira 1996), and southern Australia (Bruce 1992, Strong et al. 1996). Off the Pacific coast of North America, capture records suggest that higher proportions of adult (mature) male white sharks occur to the north whereas more juveniles and adult females have been recorded to the south, although this sex-specific pattern was not statistically significant (Klimley 1985). Speculation on sex-specific segregation in the white and other sharks has focused on sex-specific roles in reproduction (Gilmore 1993); however, annual reproductive behavior patterns at the population level are poorly understood.

White sharks occur at the South Farallon Islands (SFI), located 48 km off San Francisco, California, during autumn (primarily September-November) to prey on pinnipeds but are absent there during spring (Ainley et al. 1985, Klimley et al. 1992, Pyle et al. 1996). Although both male and female white sharks have been recorded inter-seasonally at SFI (Klimley and Anderson 1996), it is unknown whether or not sex-specific segregation patterns occur. Here we report a temporal, sex-specific occurrence pattern among adult white sharks at SFI based on examination of inter-seasonal return patterns of known-sex individuals.

METHODS

From 1987 through 2000, during daily observations in autumn (1 September to 30 November), we identified and documented individual white sharks using size and unique markings such as scars, mutilated fins, natural pigmentation patterns (which remain static from year to year; pers. obs.), and the distribution of notches on the trailing edge of the dorsal fin. From 1987 to 1992, sharks were documented with still photographs (Anderson and Goldman 1996) and shore-based video recorders (Klimley and Anderson 1996). By 1993 we discovered that white sharks investigated small (< 6 m) vessels or decoys (Anderson et al. 1996), particularly during and up to 2 hours subsequent to feeding events on pinnipeds. This behavior allowed us to employ underwater video recorders mounted on poles to document individual sharks and confirm sex by the presence (male) or absence (female) of claspers (Pratt 1996). The absence of claspers was sometimes difficult to confirm; thus, sharks were only sexed as female using adequate video-documentation of the shark's ventral region. The analysis presented here includes all individual adult sharks that 1) had distinctive features allowing confirmed identification, 2) were observed in 2 or more years, and 3) were of known sex.

RESULTS

During the 14-yr study period, we made 239 observations of 22 distinctively marked white sharks (8 females and 14 males) recorded during 2 or more years (Table 1). These sharks ranged from 3.2 to 5.9 m total length, as estimated by comparison with our 4.2-m and 5.2-m research vessels. Of these observations, 82 (34.3%) were of females and 157 (65.7%) were of males, a 1:1.91 ratio. When inter-seasonal occurrence patterns are examined (Table 1), all 8 females were observed during odd-numbered years or even-numbered years but not both, and all 14 males were observed in both odd- and even-numbered years. This sex-specific difference was highly significant (Pearson's 2 = 22.0, P < 0.0001); thus, male white sharks appear to have an annual occurrence pattern at SFI in contrast to the biennial pattern of females. Our observed sex ratio of 1:1.91 (females to males) can therefore be explained by this sex-specific pattern occurring within a population of balanced sex ratio: each year all of the males but only half of the females of the SFI population are present.

DISCUSSION

Previous reports that female white sharks occurred in consecutive years at SFI (Klimley and Anderson 1996) were likely based on misidentified or mis-sexed sharks from land-based video recordings and visual observation only (A.P. Klimley, pers. comm.). For example, shark "CC", labeled female in Klimley and Anderson, is male 8801 of this paper (claspers repeatedly confirmed with underwater video recordings), and the observation in 1992 of the female shark "AC" of Klimley and Anderson (8901 of this paper) was very likely based on a mis-identification of the male 9601. Sharks 8901 and 9601 had very similar mutations to the caudal fin and 9601 was frequently recorded in

Table 1. Number of observations each year of individual white sharks at the South Farallon Islands, California.[1]

Shark	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
A. Females														
8901			2		6		7		1					
8902			1		1		5							
8903			1		1		1							
8904			2		1		3		5					
9201						10				11		2		4
9203						4		2		3				
9401								2		2				
9801												2		3
B. Males														
8701	1				1		1			3		1		
8801		1		1		1	2	2		6		4	1	1
8802		1		3	15	16		2						
9001				1		1	1							
9101					3			2		4				
9202						3		3	4	2		3	1	
9301							1	5	7	1		1	5	4
9302							4	1		3		1		
9306							1	4		5				
9502									3			2		
9601										3	1			
9602										3	1		1	1
9901													2	2
9902													3	1

[1]An "observation" is defined as at least one sighting of an individual on a particular date.

the location of the 1992 sighting (see Klimley and Anderson 1996), whereas 8901 was never recorded in that vicinity and would be unexpected there (see Goldman and Anderson 1999). Repeated documentation of many individuals between 1993 and 2000 with video-recorders indicated that no females were present in consecutive years (Table 1).

The gestation period and length of reproductive cycle in mature female white sharks remains unknown. Studies of pregnant females off Australia and New Zealand suggest that both copulation and parturition occur there in the austral spring and summer (Francis 1996). Francis speculated that copulation might occur immediately subsequent to parturition, and that females might be able to carry successive litters with little or no resting period, but acknowledged that this needed to be demonstrated. Alternatively, the biennial occurrence of adult female white sharks at SFI suggests a 2-year reproductive cycle, during which either gestation is prolonged (> 1 yr) or copulation occurs well after parturition. Mollett et al. (2000) summarize evidence suggesting prolonged gestation periods (up to 18-24 months) and 2-year or 3-year reproductive cycles in several species of large sharks. Their speculation of an 18-month gestation for the white shark would be consistent with the 2-year reproductive cycle indicated by our data. A biennial reproductive cycle would result in a lower reproductive potential in this species than previously thought (litter sizes of only 4-11 pups have been reported; Francis 1996), which has important implications for the conservation of this species, particularly from the effects of incidental mortality (Wintner and Cliff 1999).

Based on capture data, Klimley (1985) suggested that both female and male white sharks moved northward from southern California waters into northern California waters as they matured (to 3-4 m length) and began to feed on marine mammals. Females appeared subsequently to return to southern California waters to pup whereas males remained in northern California waters. Although our data are not inconsistent with this hypothesis, recent evidence (Boustany et al. 2002, unpubl. data) indicates that both male and female white sharks can travel from SFI into the central Pacific Ocean during the spring and summer. Pregnant females may be acquiring and storing energy during the autumn at SFI for parturition and copulation the following spring and summer, after which it may take them a full year to return to northern California to gain energy for a subsequent reproductive attempt. Alternatively, females could travel from SFI to the central Pacific well off Baja California (see Boustany et al. 2002) for copulation, after which they may travel to an unknown location for parturition before returning to SFI 18-20 months later. In either case, female white sharks could potentially travel significant distances in the North Pacific Ocean during a biennial reproductive cycle to give birth, whereas copulation may occur closer to northern California, allowing males to return annually to SFI. Pregnant females have been captured in the western Pacific ocean (Bruce 1992, Francis 1996, Uchida et al. 1996) but are thus far unknown from the eastern North Pacific.

Recent genetic evidence suggesting that female white sharks in the Southern Hemisphere are philopatric whereas males travel widely (Pardini et al., 2001) appears to differ from our results. Based on our observational data, we suggest either that the genetic evidence indicates long-term, natal-dispersal patterns at the population level (as opposed to the short-term migration patterns at the individual level reported here), or that differing migration or reproductive strategies occur in different populations of the species. We are currently deploying long-term (9-12 month) satellite transmitters on female and male white sharks at SFI to better understand sex-specific occurrence patterns in the North Pacific.

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