

Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia

R. L. ROBBINS

*Department of Environmental Sciences, University of Technology, Sydney,
NSW 2006, Australia*

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The seasonal temporal sexual segregation of white sharks *Carcharodon carcharias*, at the Neptune Islands, South Australia, is described in relation to environmental variables. A significant sexual segregation was found at this site with sex ratios strongly favouring males overall. Males were more prevalent than females in all months in a 3 year sampling period, aside from April and May. There was a significant difference between the sexes in terms of mean daily numbers over the months of the study. It was also observed that sexual segregation fluctuated for unknown reasons on a temporal scale. Predictive models for estimating male and female numbers based on a series of abiotic factors were generated. Sea surface temperature, tidal height, tidal range, moon phase, cloud cover, underwater visibility and swell height were related to daily sightings of male and female white sharks to determine the influence of these variables on sexual segregation. Visibility and sea surface temperature affected male numbers, however, visibility did not affect sexual segregation. Tidal height was significantly different between males and females. Sea surface temperature also appeared to be related to sexual segregation in this species. Females were present when temperatures ranged from 15.7 to 18.1° C whereas males were observed at temperatures ranging from 14.3 to 17.8° C, with a peak in sightings in September, when sea surface temperatures were at their lowest. Since parturition is thought to occur in spring or summer, it is suggested that females are absent at this time and only return during prime feeding periods or times at which temperatures are elevated in order to increase developmental growth rates of their young. The significantly lower temperatures in 2003 may explain the absence of females in this year. Hypotheses related to temperature regulation in this species are put forward to explain the sexual segregation observed.

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Key words: abiotic; shark; temperature; tidal.

INTRODUCTION

Sexual segregation occurs when males and females occupy different habitats or social groups. Sexual segregation appears nearly universal in sharks (Bres, 1993), including the grey reef shark *Carcharhinus amblyrhynchos* (Bleeker) (Economakis & Lobel, 1998), the scalloped hammerhead *Sphyrna lewini* (Griffith & Smith)

Present address: 895 Ackland Hill Road, Coromandel East, SA 5157, Australia. Tel.: +61882705575; fax: +61882705575; email: rachelrobbins@aapt.net.au

(Klimley, 1987), the basking shark *Cetorhinus maximus* (Gunnerus) (Watkins, 1958; Lien & Fawcett, 1986), the salmon shark *Lamna ditropis* Hubbs & Follett (Blagoderov, 1994; Goldman, 2000), the blue shark *Prionace glauca* (L.) (Pratt, 1979), the tiger shark *Galeocerdo cuvier* (Péron & Lesueur) (Hiethaus, 2001) and the nurse shark *Ginglyostoma cirratum* (Bonnaterre) (Carrier *et al.*, 1994). Sexual segregation in elasmobranchs occurs for a variety of reasons including intraspecific competition, prey availability, refuge from mating, reproductive strategies associated with pre- or post-mating behaviours, or through differing seasonal habitat and resource requirements (Sims *et al.*, 2001). Sexual segregation has been anecdotally cited in white sharks *Carcharodon carcharias* (L.) (Bruce, 1992; Klimley *et al.*, 1992; Goldman & Anderson, 1999). Seasonal segregation in this species may be due to prey availability, differing physiological needs relating to abiotic variables such as sea surface temperature, or reproductive habits. Gravid females may move inshore to give birth where the warmer waters are more conducive to pupping and where cannibalism of neonates by adult males is minimized (Fergusson, 1996). If this is the case, they are therefore segregated from males at this point of their life history. Pregnant females have been caught off the west coast of South Australia in October and November (Bruce, 1992). The capture of 21 small juvenile white sharks (100–150 cm total length, L_T) in Australian waters, which were most frequently caught between December and May (Malcolm *et al.*, 2001), suggests that pupping occurs in late spring and summer.

Little is known about the mechanisms and function of sexual segregation in most species because sexual segregation, although widespread, is still little researched in most taxa where it occurs, except for unguulates (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2002). While previous studies have suggested that abiotic factors play a role in segregation, these factors have not previously been quantified. Sea surface temperature plays a role in sexual segregation of the grey reef sharks (Economakis & Lobel, 1998) of *Carcharhinus* species in the southern African seas (Bass *et al.*, 1973) and in adult small-spotted catsharks *Scyliorhinus canicula* (L.) (Compagno, 1984; Muñoz-Chápuli, 1984). White shark behaviour and abundance have been linked to abiotic variables such as water temperature, visibility and ocean currents (Ainley *et al.*, 1981; Casey & Pratt, 1985; Strong *et al.*, 1992). White shark sightings off the coast of California have been correlated with lunar phase, swell height, sea surface temperature and water clarity (Pyle *et al.*, 1996). Seasonal variations in sea surface temperature appear to play a role in the abundance and movements of white sharks. Records from boreal waters of the eastern North Pacific show white sharks occur at sea surface temperatures of 5–16° C, with most occurring where sea surface temperatures were between 9–10° C (Martin, 2004). In Florida, white sharks seem only to be present between the months of January and April, during winter and early spring (Adams *et al.*, 1994). At this time, water temperatures are at the lowest for this region and range between 18.7 and 21.6° C (Adams *et al.*, 1994). White sharks have not been recorded at other times of year, suggesting that they move into these waters only when temperatures decrease sufficiently. Mediterranean white sharks seemingly vanish from selected areas when temperatures exceed 25° C although they may remain deep in the isothermal waters, only coming to the surface sporadically (Fergusson, 1994). Large white

sharks are found to occur seasonally at the Farallon Islands, exhibiting a strong peak in the autumn months (Ainley *et al.*, 1985). They are virtually absent outside this period but it has been suggested that mature adults migrate to water off Baja from March to June in order to pup. This could lead to sexual segregation whereby mature females segregate from the rest of the population in order to travel to these areas to pup; the absence of males may reduce the risk of cannibalism of neonates (Springer, 1967). Predatory attacks by white sharks on elephant seals increases with increased tidal height (Pyle *et al.*, 1996). Through land observations, it has been determined that predatory attacks by white sharks on northern elephant seals *Mirounga angustirostris* are more frequent during higher tides than at lower tides (Anderson *et al.*, 1996). Goldman *et al.* (1996) found that white sharks were more active on days when tidal fluctuations were large (1–2 m) suggesting tidal range might also influence abundance. White shark sightings have been found to increase with periods of decreased moonlight, increased cloud cover and increased swell height (Pyle *et al.*, 1996), which may act to increase the white shark's hunting success by allowing better camouflage, or by forcing prey into the water and decreasing haul-out space for northern elephant seals.

The objective was to determine whether sexual segregation is characteristic of the white sharks in the study area, and to establish the relative importance of sea surface temperature, swell height, tidal height, tidal range, moon phase, cloud cover and underwater visibility in determining the distribution and abundance of male and female white sharks at the Neptune Islands. It is hypothesized that females will be more prevalent with increased tidal height, tidal range, cloud cover and swell height, and with decreased moon phase and underwater visibility. This is due to the increased hunting opportunities coupled with displacement of the males by the more dominant, larger females during these times.

MATERIALS AND METHODS

The Neptune Islands lie at the mouth of the Spencer Gulf off Port Lincoln, South Australia, and consist of two island groups: North Neptune Islands (35°14' S; 136°04' E) and South Neptune Islands (35°20' S; 136°06' E). The Neptune Islands are separated from inshore islands by a seasonally dominant frontal zone at the mouth of the Spencer Gulf, which is most prominent in summer and autumn (Nunes & Lennon, 1986). As well as being significant areas for white sharks, the Neptune Islands are the feeding area and nationally significant breeding area for New Zealand fur seals *Arctocephalus forsteri* and Australian sea lions *Neophoca cinerea* (Robinson *et al.*, 1996). Expeditions were conducted from April 2001 until February 2004, encompassing 27 expeditions over 140 days with each trip lasting between 4 and 11 days.

White shark densities were estimated based on attraction to bait. White sharks were attracted to the boat by means of a standardized baiting method (Strong *et al.*, 1992). A three-dimensional odour corridor was discharged consisting of known amounts of chum mixture of unrefined fish oil, minced southern blue fin tuna *Thunnus maccoyii* (Castelnaud) and its blood, and sea water, delivered at a low rate. Baits of whole Australian salmon (*Arripis* sp.) or southern blue tuna chunks (weighing *c.* 1 kg) were attached to a natural fibre bait line *c.* 15 m in length and allowed to drift from the stern of the boat. Once a white shark arrived and showed interest in the baits, the baits were drawn closer to the boat by crew members to allow tagging, identification and

photography to take place. The sex was noted from the presence or absence of claspers, the male reproductive organ, by observations both on deck and underwater. White sharks were also identified through use of a photographic database.

Environmental variables examined were sea surface temperature, swell height, underwater visibility, cloud cover, tidal height, tidal range and moon phase. Variables were recorded at 0900, 1200, 1500 and 1800 hours each day. To obtain daily measurements of these variables, the data points for each day were averaged. Sea surface temperature was measured at a consistent location on the vessel, 1 m below the surface, using a calibrated temperature probe. It was ensured that readings were taken up current from the chum dispenser so that the colder temperature of the chum mixture did not interfere with the true sea surface temperature. Whilst onshore, readings from the Neptune Islands, Spencer Gulf, Gulf St Vincent and Ceduna were also taken, using remote sensing satellite imagery (CSIRO Marine Research, 2001–2003). Swell height and underwater visibility (horizontal distance) were measured on a rank scale of 1–5, 1 being the lowest and 5 being the highest. Swell height was estimated from local weather reports for the given area, as heard daily from the ship's radio, in conjunction with observed heights within the specific site of the mooring. Underwater visibility was scored on a rank scale using the visual underwater distance of known objects as a measure, such as certain points on the hull of the vessel. Cloud cover was recorded by estimating the percentage of sky obscured by cloud to the nearest 10%. Local tidal heights and ranges were determined for each day on location using the computer software programme Seafarer Tides® (Commonwealth of Australia). Tidal range was defined as the difference between the highest and lowest tides on each particular day. Moon phase was calculated using the computer software programme Moontool 0.9 (2002) (Microsoft) and was classified as the percentage fullness of the moon, with 0% being a new moon and 100% being a full moon.

ANALYSES

The number of white sharks observed per hour of baiting was calculated to allow comparison with a previous study. This method gave a measurement analogous to catch per unit effort (CPUE) (Strong *et al.*, 1996). Repeated sightings of individual white sharks in any month were removed prior to analysis of data sets. To correct for variations in the number of sampling days for each month (*i.e.* to correct for effort), the mean daily number of white sharks for each month was calculated. A Kolmogorov–Smirnov test was conducted and data were transformed to conform to assumptions. The data were used in analyses of seasonal differences in the numbers of each sex using a three-factor ANOVA (factors: sex, month and year). The sex ratio was calculated, and compared with the expected ratio of 1:1 (no sexual segregation) using a χ^2 -test.

The effects of environmental variables on white shark abundance and segregation were also investigated. First, the variables were tested for multicollinearity using linear regressions, and certain related variables were then excluded from analyses. Using the number of white sharks of each sex observed per day, linear multiple regressions were conducted to examine the relationships between the number of males or females (dependent variables) and sea surface temperature, tidal height, tidal range, underwater visibility, swell height, moon phase and cloud cover (independent variables). Spearman correlations (r_s) were conducted on the ranked swell height and underwater visibility data and the abundance of each sex, whilst Pearson correlations (r) were conducted on all other remaining independent variables. As strong correlations were found between specific independent variables, a stepwise elimination method (Sokal & Rohlf, 1981) was used to assess which variables had the strongest correlation with the dependent variable. Stepwise multiple regressions allowed 'best' models for predicting white shark, female and male numbers to be selected based on the environmental factors considered. To explore the effects of the variables highlighted in the multiple regression models on sexual segregation, ANCOVA were applied. The possible relationships of tidal height and sea surface temperature to sexual segregation were investigated in this

way. Non-parametric analyses were used as the data consisted of composite counts. While not as powerful as parametric tests, the analyses used were more conservative but their validity remained.

RESULTS

A total of 126 white sharks were observed of which 92 were male (73.0%) and 32 were female (25.4%); the remaining two white sharks (1.6%) were unidentified according to sex. The overall sex ratio was biased towards males with a ratio of 3:1. Females were more abundant than males from April to June 2001 and April 2002, but males predominated for the remainder of the research period. The maximum number of females observed per day was in June 2001 ($n = 1.3$), whilst the maximum number of males encountered was in August 2001 ($n = 2.5$) (Fig. 1). The mean daily number of males was highest in September, while the mean daily number of females was highest in June for all years combined (Fig. 2). There, was a significant interaction between sex and month in relation to white shark abundance (ANOVA, d.f. = 9, 45, $P < 0.05$; Table I and Fig. 2) although *post hoc* tests failed to divide months into sub-sets. This suggested that one sex was more abundant than the other in some months, but less abundant in other months.

The main effect term in the model for female abundance was tidal height (multiple stepwise regression, d.f. = 1, $P < 0.001$; Table II), and a one-way ANOVA P value of <0.001 confirmed that there was a relationship between this variable and female numbers. Tidal range and tidal height exhibited high colinearity (linear regression, d.f. = 1, $P < 0.001$), as would be expected due

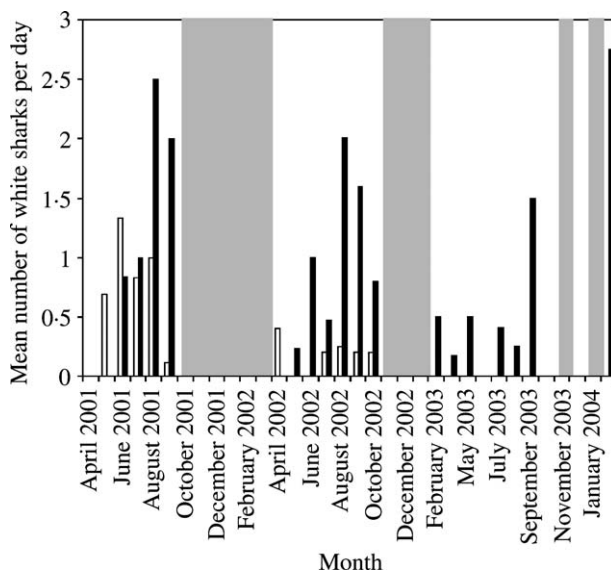


FIG. 1. Number of male (■) and female (□) white sharks encountered per day throughout the study period by month ($n = 23$) for both island groups combined. ■, the periods not covered and hence not included in the data.

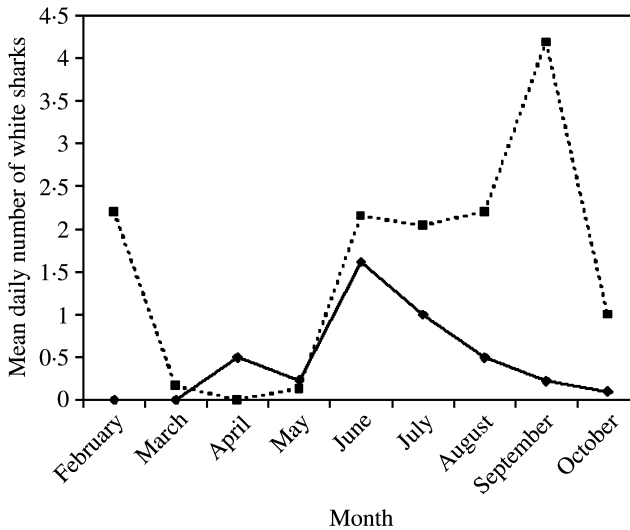


FIG. 2. Mean daily numbers of female (—◆—) and male (---■---) white sharks encountered per month for all 3 years combined ($n = 3$ years at Neptune Islands).

to the nature of the tidal cycle. As the daily tidal height increased so the tidal range also increased. Therefore, the factors related to the tidal cycle affected the model predicting female abundance, since there was high multicollinearity between tidal height and tidal range. In decreasing order of importance, visibility (multiple stepwise regression, d.f. = 1, $P < 0.05$), sea surface temperature (multiple stepwise regression, d.f. = 1, $P < 0.05$) and tidal height (multiple stepwise regression, d.f. = 1, $P < 0.05$) were the physical factors most suitable for predicting male numbers (Table II). In further analyses, however, no significant relationships between male abundance and visibility or tidal height were found. There was a negative linear relationship between the number of males

TABLE I. Three-factor ANOVA investigating the difference in abundance of each sex between the months and years of the study

Source	SS	d.f.	MS	F	P
Corrected model	1.93	6	0.322	2.342	0.073
Intercept	8E-04	1	8E-04	0.006	0.939
Sex	0.230	1	0.230	2.684	0.111
Month	5.799E-03	7	5.799E-03	0.068	0.796
Year	2.395E-02	2	1.197E-02	0.140	0.870
Sex \times month	1.098	7	0.549	3.995	0.036
Sex \times year	0.048	2	0.024	0.176	0.84
Sex \times month \times year	0.422	14	0.211	1.535	0.241
Error	3.139	39	0.08		
Total	4.743	46			

Dependent variable, \log_{10} (mean daily number of sharks per month).

TABLE II. Predictive model summaries of the environmental effects on the numbers of white sharks at the Neptune Islands, South Australia, shown by stepwise multiple regressions

All sharks			Males			Females		
Factor	<i>t</i>	<i>P</i>	Factor	<i>t</i>	<i>P</i>	Factor	<i>t</i>	<i>P</i>
Tidal height	3.574	<0.001	Vis	-2.482	0.014	Tidal height	4.096	<0.001
Vis	-3.134	0.002	SST	-2.967	0.004			
SST	-2.204	0.029	Tidal height	2.568	0.011			
Overall r^2	0.135		Overall r^2	0.115		Overall r^2	0.152	
Overall <i>P</i>	<0.001		Overall <i>P</i>	<0.001		Overall <i>P</i>	<0.001	

r^2 values represent those values for all variables combined.

SST, sea surface temperature; Vis, underwater visibility.

per day and sea surface temperature (multiple stepwise regression, d.f. = 1, $P < 0.05$; Fig. 3).

ANCOVA showed that there was a significant difference between the sexes in relation to tidal height (ANCOVA, $n = 140$, $P < 0.05$) (Fig. 4 and Table III). Female numbers seemed to be skewed towards the higher temperature ranges whereas male numbers were concentrated at slightly lower temperatures (Fig. 4), although no linear relationship existed between females and sea surface temperature. There was a significant difference between males and females in terms of sea surface temperature (ANCOVA, $n = 140$, $P < 0.05$; Fig. 4 and Table IV) suggesting it may be a contributing factor to the sexual segregation observed. Sea surface temperatures at the Neptune Islands peaked in April and May and reached a low in September and October each year. There was a significant difference between the years in terms of mean monthly sea surface temperatures (one-way ANOVA, d.f. = 2, 70, $P < 0.05$). A Student–Newman–Keuls *post hoc* test identified 2003 as significantly different from 2001 and 2002 in terms of sea surface temperature (Fig. 5).

The result from the three-factor ANOVA showed no interaction among month, year and sex in regards to daily white shark numbers (three-factor ANOVA, d.f. = 2, 45, $P > 0.05$; Table I). No significant interaction between sex and year was found (two-factor ANOVA, d.f. = 2, 45, $P > 0.05$; Table II), a result that may be confounded by the paucity of females throughout the study. Neither cloud cover nor swell height were a good predictor of the numbers of male or female white sharks observed per day. There were no significant differences between daily male and female white shark numbers in relation to underwater visibility despite the inclusion in the model for predicting male abundance; therefore this variable was not contributing to the sexual segregation observed.

DISCUSSION

Temporal sexual segregation occurred in white sharks at the Neptune Islands. A higher percentage of males were recorded for all months aside from April and May. This is in direct contrast to results found by Malcolm *et al.*

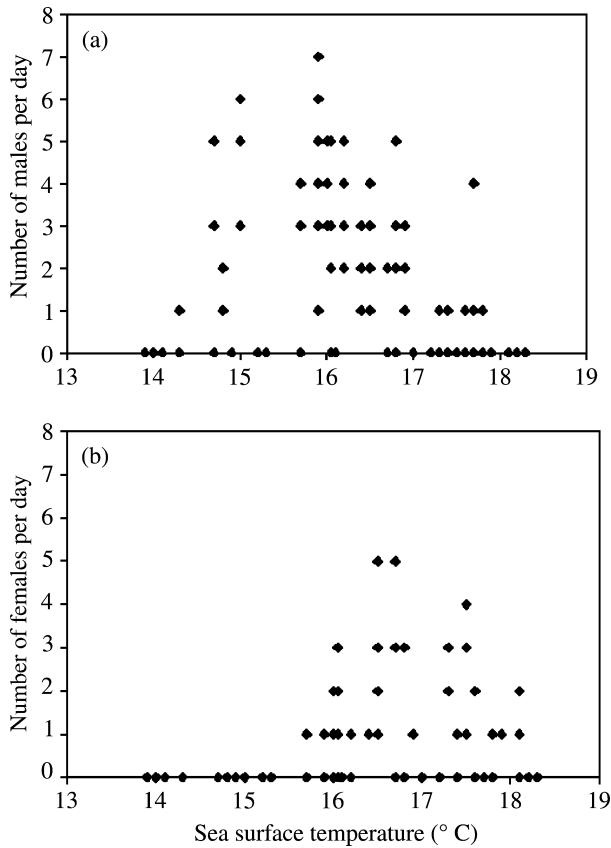


FIG. 3. Number of (a) male ($n = 92$) and (b) female ($n = 32$) white sharks observed per day as a function of sea surface temperature.

(2001) for the period August 1999 to August 2000, where males outnumbered females only in summer. Furthermore, contrary to the 3:1 male to female sex ratio recorded in this study, females were over twice as abundant as males from August 1999 to August 2000, with a male to female sex ratio of 20:58 (Malcolm *et al.*, 2001). Sex ratios in elasmobranchs are often difficult to interpret due to seasonal movement patterns (Castro, 1983; Compagno, 1984). Females were most often encountered at the Neptunes from April to June. It is at this time of the year that New Zealand fur seal pups are learning to swim, venturing further away from shore and the safety of isolated nursery pools. Being inexperienced, these pups would be easy prey in comparison to their adult counterparts (Martin *et al.*, 2005). This time of year may therefore prove to be prime hunting time for white sharks in this area.

Sea surface temperature was found to be one of the factors contributing to the sexual segregation of white sharks at the Neptune Islands, documented by the significant difference between numbers of males and females in relation to this variable. Neptune Island sea surface temperatures reached a low in September and October and peaked from February to March. Female white

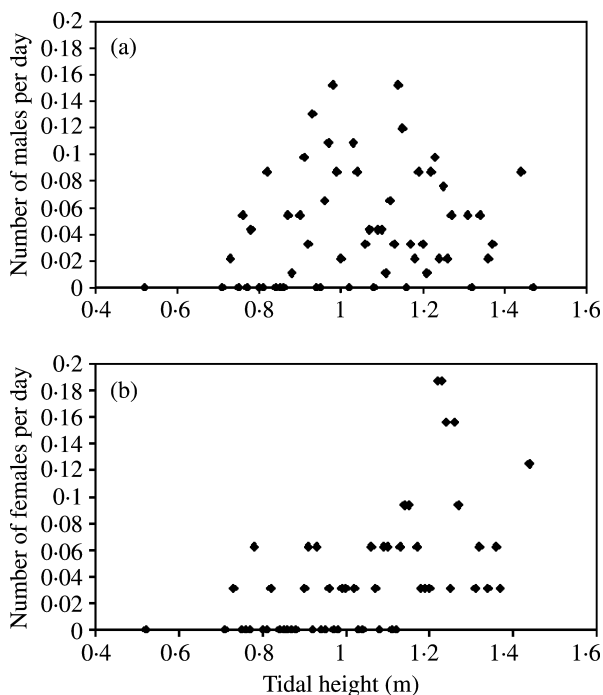


FIG. 4. Number of (a) male ($n = 92$) and (b) female ($n = 32$) white sharks observed per day in relation to tidal height.

sharks were absent from October through to February (spring to summer) with the highest number of individuals sighted in May and June (late autumn and early winter), when sea surface temperatures remain relatively high. Parturition is thought to occur in spring or summer, based on the capture of neonates and of females carrying large embryos around this time (Casey & Pratt, 1985; Klimley, 1985; Krogh, 1994; Fergusson, 1996; Uchida *et al.*, 1996). The timing of mating is also thought to be spring to summer (Bruce, 1992; Francis, 1996). During spring and early summer, mature females are probably mating or giving birth, which may aid in explaining their absence from the Neptune Islands at this time, supported by the fact that the Neptune Islands are not considered

TABLE III. Analysis of covariance using sex as the independent variable and tidal height as the covariate

Source of variation	SS	d.f.	MS	<i>F</i>	<i>P</i>
Corrected model	846.746	59	14.352	2.274	0.001
Intercept	29.953	1	29.953	4.746	0.033
Tidal height	618.814	58	10.669	1.690	0.024
Error	366.068	58	6.312		
Total	1996.000	118			

Dependent variable, number of white sharks.

TABLE IV. Analysis of covariance using sex as the independent variable and sea surface temperature as the covariate

Source of variation	SS	d.f.	MS	F	P
Corrected model	308.472	37	8.337	4.903	<0.001
Intercept	34.207	1	34.207	20.115	<0.001
SST	187.558	36	5.210	3.064	<0.001
Error	411.528	242	1.701		
Total	1000.000	280			

Dependent variable, number of white sharks ($r^2 = 0.428$).

to be mating or nursery grounds for this species (Malcolm *et al.*, 2001). This would leave an open niche for males and subadults to exploit during this period, until such a time that the females return, as evidenced by the higher number of males observed at lower temperatures. Females became more prevalent in April and may have been competitively excluding smaller conspecifics and males from the area. This is supported by Strong *et al.* (1996), who noticed a size-based feeding hierarchy whereby individuals deferred to larger conspecifics during direct interactions, and appeared to limit their use of the area in order to avoid larger individuals. The absence of females in 2003 may be due to significantly lower temperatures in this year, providing further evidence for the temperature related sex ratio differences observed. White shark sightings peaked at higher temperatures in studies in South Africa, and decreased rapidly when temperatures reached 11–13° C (Ferreira & Ferreira, 1996). As the sex ratios observed in South Africa were heavily biased towards females, it was suggested that there were more females at these higher temperatures than at lower temperatures (Ferreira & Ferreira, 1996), thus confirming the sea surface temperature related findings here.

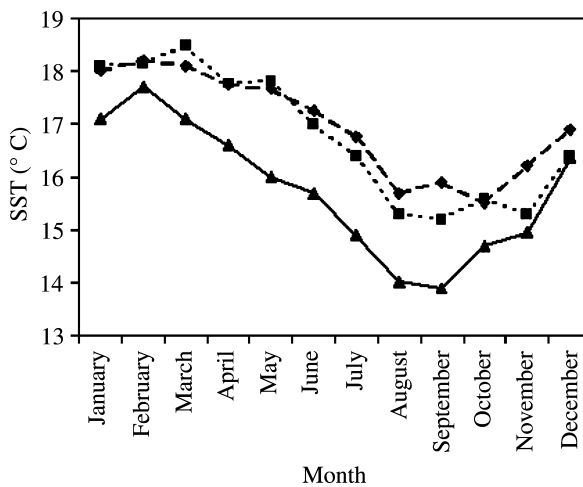


FIG. 5. The differences between the monthly sea surface temperatures (SST) at the Neptune Islands for each year of the study (◆, 2001; ■, 2002; ▲, 2003).

Correlations between temperature and the abundance and distribution of other elasmobranch species have been previously noted (Economakis & Lobel, 1998; Hopkins & Cech, 2003). Development rate of embryonic young has been found to increase with increased maternal body temperature in most ectotherms (Precht *et al.*, 1973) and has been suggested as a stimulator for aggressive behaviours in some elasmobranch species (Harris, 1952; Taylor, 1993). Females may be favouring the warmer Neptune Islands during winter (since the waters of the South Australian Gulfs are colder than those at the Neptune Islands in winter) in order to increase their internal temperatures and hence increase their growth rates and the developmental rate of embryonic young, as observed in the grey nurse shark *Carcharias taurus* Rafinesque (Bass, 1978) and the grey reef shark (Economakis & Lobel, 1998). Females of these shark species that segregate by sex grow faster and larger than males and reach sexual maturity at a size greater than males but, in species where sexual segregation does not occur, differential growth rates are not observed (Klimley, 1987). Segregation by sex may be expected using Klimley's (1987) criteria since female white sharks grow larger and attain maturity at a greater size than males. Moreover, females may therefore be achieving a faster growth rate than males by favouring waters of higher temperatures in order to increase their body temperature (Economakis & Lobel, 1998), although there is no direct evidence of this in the white shark. Ontogenetic shifts in temperature preferences have been previously demonstrated in teleost species (Magnuson *et al.*, 1979; McCauley & Huggins, 1979; Coutant, 1985) and behavioural thermoregulation has also been suggested for some elasmobranch species (Compagno, 1984; Carey & Scharold, 1990; Castro, 1993; Hopkins & Cech, 1993; Morrissey & Gruber, 1993; Economakis & Lobel, 1998; Hopkins & Cech, 2003), both of which may also be influencing sexual segregation of white sharks.

Whilst female abundance was primarily affected by the tidal cycle, it only accounted for 15.2% of variation in female numbers, possibly since the Neptune Islands do not represent a closed environment and other factors not considered may have influenced white shark movements. The abundance of females was skewed towards the higher recorded tidal heights. The reduced haul-out space for pinnipeds during higher tides would result in increased numbers of prey being forced into the water, and hence may create a hunting environment with an increased success rate for white sharks. The generally larger females may exclude smaller males during these times of higher tides in order to monopolize on the easier hunting conditions, which could account for the sexual segregation observed. This relationship, however, proved relatively weak and other factors are likely to come into play.

The conclusions drawn here are based on the population at the Neptune Islands only and so spatial segregation cannot be ascertained. A broader spatial segregation in Australian waters cannot be assumed without data from other sites therefore further work should encompass other sites in their range. Considerable seasonal and interannual variability have been reported historically at this site (R. Fox, pers. comm.) so data from further years may provide a more accurate picture of sexual segregation. A long-term measure of abundance is needed, which considers results from multiple years and decades in order to measure the true abundance, taking into account any fluctuations that

may occur. The continuance of a listening station project (Bruce & Stevens, 2003) would help to diminish the possible error in counts due to unobserved white sharks. White sharks possessing sonic tags would register on these stations when they are in the area, which, in conjunction with data taken on site, would give an indication of the likelihood of a white shark not being detected by onboard observers whilst in the area. Further studies should also focus on determining the local and long-term movements of white sharks of both sexes once they leave the Neptune Islands, and whether the sexual segregation is observed throughout their range or only at feeding sites.

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References

- Adams, D. H., Mitchell, M. E. & Parsons, G. R. (1994). Seasonal occurrence of the white shark, *Carcharodon carcharias*, in waters off the Florida west coast, with notes on its life history. *Marine Fisheries Review* **56**, 24.
- Ainley, D. G., Strong, C. S., Huber, H. R., Lewis, T. J. & Morrell, S. H. (1981). Predation by sharks on pinnipeds at the Farallon Islands. *Fishery Bulletin* **78**, 941–945.
- Ainley, D. G., Henderson, R. P., Huber, H. R., Boekelheide, R. J., Allen, S. G. & McElroy, T. L. (1985). Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *Memoirs of the Southern California Academy of Sciences* **9**, 109–122.
- Anderson, S. D., Klimley, A. P., Pyle, P. & Henderson, R. P. (1996). Tidal height and white shark predation at the Farallon Islands, California. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 275–279. New York: Academic Press Inc.
- Bass, A. J. (1978). Problems in studies of sharks in the southwest Indian Ocean. In *Sensory Biology of Sharks, Skates, and Rays* (Hodgson, E. S. & Mathewson, R. F., eds), pp. 545–594. Arlington, VA: Office of Naval Research.
- Bass, A. J., D'Aubrey, D. & Kistnasamy, N. (1973). Sharks of the east coast of southern Africa. *International Oceanographic Research Institute* **33**, 1–168.
- Blagoderov, A. I. (1994). Seasonal distribution and some notes on the biology of the salmon shark (*Lamna ditropis*) in the northwestern Pacific Ocean. *Journal of Ichthyology* **34**, 115–121.
- Bres, M. (1993). The behaviour of sharks. *Reviews in Fish Biology and Fisheries* **3**, 133–159.
- Bruce, B. D. (1992). Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. *Australian Journal of Marine and Freshwater Research* **43**, 1–11.
- Bruce, B. D. & Stevens, J. D. (2003). Site fidelity, residence times and home range patterns of white sharks around pinniped colonies. *Report Record No. 346086*. Hobart: CSIRO Marine Research.
- Carey, F. G. & Scharold, J. V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology* **106**, 329–342.
- Carrier, J. C., Pratt, H. L. & Martin, L. K. (1994). Group reproductive behaviours in free-living nurse sharks, *Ginglyostoma cirratum*. *Copeia* **1994**, 646–656.
- Casey, J. G. & Pratt, H. L. (1985). Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Memoirs of the Southern Californian Academy of Sciences* **9**, 2–14.

- Castro, J. L. (1983). *Sharks of North America Waters*. College Station, TX: Texas A and M University Press.
- Castro, J. L. (1993). The biology of the finetooth shark, *Carcharhinus isodon*. *Environmental Biology of Fishes* **36**, 219–232.
- Compagno, L. J. V. (1984). FAO Species Catalogue, Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis* **125**.
- Coutant, C. C. (1985). Striped bass, temperature and dissolved oxygen: a speculative hypothesis for environmental risk. *Transactions of the American Fisheries Society* **114**, 31–61.
- Economakis, A. E. & Lobel, P. S. (1998). Aggregation behaviour of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes* **51**, 129–139.
- Fergusson, I. K. (1994). Notes on the shark fauna of the Sicilian Channel, with reference to future in-situ studies by means of tagging. In *Proceedings of the 2nd European Shark & Ray Workshop* (Fowler, R. C. & Earll, S. L., eds), p. 83. London: British Museum (Natural History).
- Fergusson, I. K. (1996). Distribution and autecology of the white shark in the eastern North Atlantic Ocean and the Mediterranean Sea. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 321–345. New York: Academic Press Inc.
- Ferreira, C. A. & Ferreira, T. P. (1996). Population dynamics of white sharks in South Africa. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 381–391. New York: Academic Press Inc.
- Francis, M. P. (1996). Observations on a pregnant white shark with a review of reproductive biology. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 157–172. New York: Academic Press Inc.
- Goldman, K. (2000). Distribution, segregation, and the potential for variable growth rates in the salmon shark, *Lamna ditropis*, in the western and eastern North Pacific. Abstract. *80th Meeting of the American Society of Ichthyologists and Herpetologists and 16th Meeting of the American Elasmobranch Society, La Paz, Baja, Mexico* (Bruner, J., ed.), p. 2. Gainesville, FL: American Elasmobranch Society.
- Goldman, K. J. & Anderson, S. D. (1999). Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, Central California. *Environmental Biology of Fishes* **56**, 351–364.
- Goldman, K. J., Anderson, S. D., McCosker, J. E. & Klimley, A. P. (1996). Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 111–120. New York: Academic Press Inc.
- Harris, J. E. (1952). A note on the breeding season, sex ratio and embryonic development of the dogfish, *Scyliorhinus canicula*. *Journal of the Marine Biological Association of the United Kingdom* **31**, 269–275.
- Hiethaus, M. R. (2001). Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology* **253**, 53–68.
- Hopkins, T. E. & Cech, J. J. Jr (1993). Effect of temperature on oxygen consumption of the bat ray, *Myliobatis californica*, (Chondrichthyes, Myliobatidae). *Copeia* **1994**, 529–532.
- Hopkins, T. E. & Cech, J. J. Jr (2003). The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environmental Biology of Fishes* **66**, 279–291.
- Klimley, A. P. (1985). The areal distribution and autecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Memoirs of the Southern California Academy of Sciences* **9**, 15–40.
- Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* **18**, 27–40.

- Klimley, A. P., Anderson, S. D., Pyle, P. & Henderson, R. P. (1992). Spatiotemporal patterns of white shark, *Carcharodon carcharias*, predation at the South Farallon Islands California. *Copeia* **1992**, 680–690.
- Krogh, M. (1994). Spatial, seasonal and biological analysis of sharks caught in the New South Wales protective beach meshing program. *Australian Journal of Marine and Freshwater Research* **45**, 1087–1106.
- Lien, J. & Fawcett, L. (1986). Distribution of basking sharks *Cetorhinus maximus* incidentally caught in inshore fishing gear in Newfoundland. *Canadian Field-Naturalist* **100**, 246–252.
- Magnuson, J. J., Crowder, L. B. & Medvick, P. D. (1979). Temperature as an ecological resource. *American Zoologist* **19**, 331–343.
- Malcolm, H., Bruce, B. D. & Stevens, J. D. (2001). A review of the biology and status of white sharks in Australian waters. *Report Record No. 304835*. Hobart: CSIRO Marine Research.
- Martin, R. A. (2004). Northerly distribution of white sharks, *Carcharodon carcharias*, in the eastern Pacific and relation to ENSO events. *Marine Fisheries Review* **66**, 16–26.
- Martin, R. A., Hammerschlag, N., Collier, R. S. & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom* **85**, 1121–1135.
- McCauley, R. W. & Huggins, N. W. (1979). Ontogenetic and non-thermal seasonal effects on thermal preferenda of fish. *American Zoologist* **19**, 267–271.
- Morrissey, J. F. & Gruber, S. H. (1993). Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environmental Biology of Fishes* **38**, 311–319.
- Muñoz-Chápuli, R. (1984). Ethologie de la reproduction chez quelques requins de l'Atlantique Nord-Est. *Cybium* **8**, 1–14.
- Nunes, R. A. & Lennon, G. W. (1986). Physical property distributions and seasonal trends in Spencer Gulf, South Australia: an inverse estuary. *Australian Journal of Marine and Freshwater Research* **37**, 39–53.
- Pratt, H. L. (1979). Reproduction in the blue shark, *Prionace glauca*. *Fishery Bulletin* **77**, 445–470.
- Precht, H., Christophersen, J., Hensel, H. & Larcher, W. (1973). *Temperature and Life*. Berlin: Springer Verlag.
- Pyle, P., Anderson, S. D., Ainley, D. G. & Henderson, R. P. (1996). Environmental factors affecting the occurrence and behaviour of white sharks at the Farallon Islands, California. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 281–291. New York: Academic Press Inc.
- Robinson, A. C., Cauty, P. D., Mooney, P. A. & Ruddock, P. M. (1996). *South Australia's Offshore Islands*. Adelaide: South Australian Department of Environment and Natural Resources.
- Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* **56**, 99–106.
- Ruckstuhl, K. E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* **77**, 77–96.
- Sims, D. W., Nash, J. P. & Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology* **139**, 1165–1175.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*, 2nd edn. San Francisco, CA: Freeman.
- Springer, S. (1967). Social organization of shark populations. In *Sharks, Skates and Rays* (Gilbert, P. W., Mathewson, R. F. & Rall, D. P., eds), pp. 149–174. Baltimore, MD: John Hopkins Press.
- Strong, W. R., Murphy, R. C., Bruce, B. D. & Nelson, D. R. (1992). Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. *Australian Journal of Marine and Freshwater Research* **43**, 13–20.
- Strong, W. R., Bruce, B. D., Murphy, R. C. & Nelson, D. R. (1996). Population dynamics of white sharks in Spencer Gulf, South Australia. In *Great White Sharks:*

- the Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 401–414. New York: Academic Press.
- Taylor, L. (1993). *Sharks of Hawaii: Their Biology and Cultural Significance*. Honolulu, HI: University of Hawaii Press.
- Uchida, S., Toda, M., Teshima, K. & Yano, K. (1996). Pregnant white sharks and full-term embryos from Japan. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 139–155. New York: Academic Press Inc.
- Watkins, A. (1958). *The Sea My Hunting Ground*. London: Heinemann.

Electronic Reference

- CSIRO Marine Research. (2001–2003). *CSIRO Marine Research Remote Sensing*. Available at http://www.marine.csiro.au/~lband/web_point/