# Segregation or aggregation? Sex-specific patterns in the seasonal occurrence of white sharks at the Neptune Islands, South Australia

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## Abstract

We reviewed the seasonal patterns of occurrence of male and female white sharks at the Neptune Islands in South Australia, where some of Australia's largest pinniped colonies are located. Analyses of our 14-year data series indicate that females seasonally aggregate in late autumn and winter coinciding with the maximum in-water availability of lactating female New Zealand seals and seal pups. Although male sharks occurred in approximately equal numbers to females during this period, some males also visited throughout the year and their overall abundance generally peaked during summer when females were absent. These differences suggest that foraging strategies/prey selection differ between sexes in white sharks across the life-history stages represented. There was little evidence for segregation by sex or size at the Neptunes, but the highly focused seasonal pattern of occurrence by females compared to the year-round visits by males suggests that there are likely to be differences between the sexes in overall distribution and movements patterns across southern Australia. Our data suggest that sex-specific foraging strategies may play an important role in structuring movement patterns in white sharks. Differences between sexes in distribution, movement patterns and foraging strategies are likely to have implications for modelling the consequences of fisheries by-catch between regions or jurisdictions and other spatially or temporally discrete anthropogenic impacts on white shark populations. Such differences would also suggest a need to treat the sexes separately in population and movement models as well as under recovery plan actions.

## Introduction

Segregation by sex and life-history stage is a widespread trait of many terrestrial and marine populations (Sims 2005, Martin and da Silva 2004, Ruckstuhl and Neuhaus 2002). Segregation is considered to be a common feature of elasmobranch populations and was recently reviewed by Wearmouth and Sims (2008) who concluded that, despite its generality, the underlying causes remain poorly understood. Segregation, where it results in different patterns of distribution, habitat use, exploitation rates or other anthropogenic impacts between sexes, is an important factor to consider when modelling commercially valuable elasmobranch populations (Mucientes *et al.* 2009) as well as when developing recovery and monitoring strategies for species of conservation concern.

The white shark (*Carcharodon carcharias*) is a listed threatened species, protected by various national jurisdictions and international treaties such as CITES and CMS, and is the focus of a variety of research and conservation efforts over much of its global distribution (Bruce 2008). White sharks have been reported to show various patterns of segregation by sex and size on a variety of spatial and temporal scales (Kock *et al*. 2013, Domeier and Nasby-Lucas 2012, Anderson and Pyle 2003, Klimley 1985). However, the underlying reasons for these behaviours have not been determined. One of the few studies specifically examining segregation by size and sex in white sharks was that by Robbins (2007) which covered a three year period at the Neptune Islands in South Australia. These data were then re-examined by Robbins and Booth (2012). These authors reported a seasonal pattern of segregation by size and sex and a negative correlation between the presence of males and sea-surface temperature. These authors also speculated that mature pregnant white sharks may be using the warmer waters of the Neptune Islands during late summer/early autumn and that the absence of adult females in 2003 was in response to lower than average water temperatures recorded during that year. However, the short term (three year) nature of their data, the lack of year-round sampling and the relatively low number of sharks sighted during the 2001–2004 period of the study precluded substantive analyses.

The Neptune Islands hold one of the largest aggregations of pinnipeds in Australian waters (Shaughnessy and McKeown 2002) and have been the site of an active cage-dive industry for white sharks since the 1970s (Bradford and Robbins 2011). Acoustic and satellite-based telemetry tagging at the Neptune Islands have identified that white sharks may be encountered year-round (Bruce and Bradford 2013). However, despite this year-round presence, individuals are only temporary visitors to the site with relatively limited periods of residency (Bruce *et al*. 2005). Electronic and conventional tagging has revealed that sharks travel from the Neptune Islands to areas across their Australasian range including into tropical waters (Bruce *et al*. 2006) and that some return on an annual or more frequent basis (Bruce and Bradford 2013). Daily logbook records of the number of individual sharks sighted by shark cage-dive operators (SCDO) have been maintained since 1999 and these data have revealed significant seasonal and interannual differences in the total number of white sharks sighted (Bruce and Bradford 2013).

In this study, we examine a sustained long-term data series spanning 14 years of observations on white sharks at the Neptune Islands in order to further evaluate the patterns of sexual and size segregation at this site and the implications for sex-specific differences in their distribution across southern Australia. We compare these patterns to other observations on white shark residency at pinniped colonies across their global range and suggest possible driving influences based on common hypotheses used to account for sexual segregation. Significant sex-specific differences in habitat use, if not accounted for, are likely to lead to higher levels of uncertainty when modelling risk/recovery outcomes for the species.

## Methods

### Study area

The Neptune Islands (35°16.7S; 136°5.5E) are a series of granite formations rising steeply from approximately 60–100 m depth on the continental shelf some 60–70 km south of Port Lincoln, South Australia (Figure 1). The island system comprises two groups, the North and South Neptune Islands, which are approximately 12 km apart. Each island group comprises two main islands and various small rock outcrops. A shark cage-dive industry has been operating predominantly at the North Neptune Islands since the late 1970s. Details of cage-dive operations and the methods used to attract sharks to the operator vessel are described by Bruce and Bradford (2013).

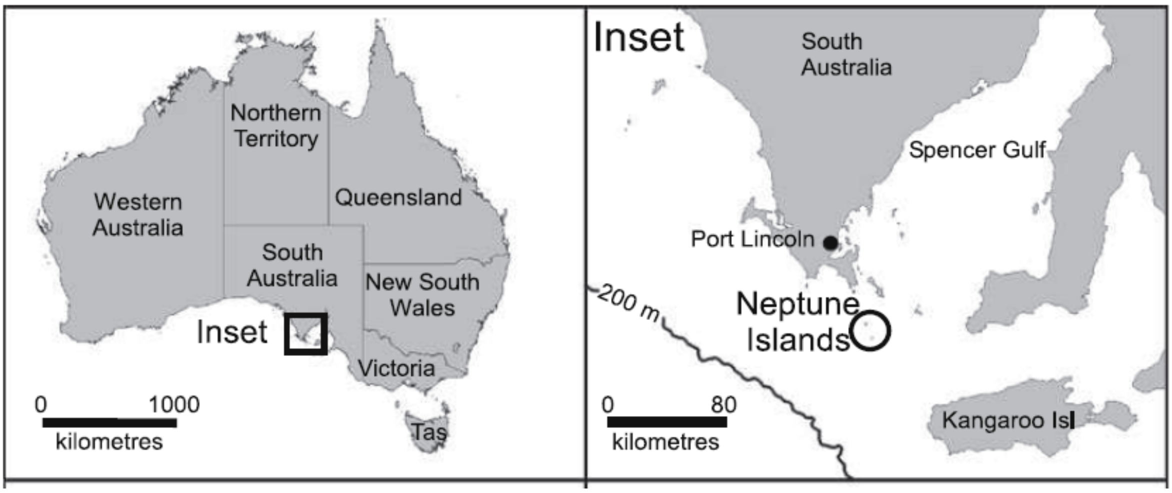

Figure 1: The location of the Neptune Islands, South Australia.

### Daily logbook data

A daily logbook system was first introduced to the shark cage-diving industry in August 1999 (Malcolm *et al*. 2001) and has since become a mandatory requirement of the license to operate. Two operators were continuously active over the study period from January 2000 to December 2013. A third operator commenced shark cage-dive operations in 2011. However, their methods to attract sharks significantly differed from the two existing operators. Given these differences, data from only the two original operators were used for analyses to maintain consistency over the period of the study. The logbook detailed the location of dive operations, arrival and departure times of vessels, the total number of sharks sighted and the sex of individual sharks. The logbook was modified in 2011 to include an estimate of length for each shark recorded. Both of the original SCDOs had many years of experience in the industry prior to the introduction of logbooks and were highly experienced in observing and identifying individual sharks as well as estimating their length. The SCDOs independently identified the number of individual sharks around their vessel each day by their size, sex, location of tags (if present) and natural marks (including shape of the posterior margin of the dorsal fin, markings on the flank and lower caudal lobe – see Robbins and Fox 2012). Assessments, including confirmation of sex, were based on both surface and underwater observations and photographs. Photo-based records have been successfully used to identify individual elasmobranchs (Marshall *et al.* 2011), including white sharks (Anderson *et al.* 2011; Nasby-Lucas and Domeier 2012) at various locations worldwide. Daily sightings data were averaged between the two operators and aggregated by month for the present study.

Logbook data were assessed on the basis of an ‘operator day’ being defined as any day that shark cage-diving operations occurred on site regardless of the number of operators present or the duration of operations on that day. In general, shark cage dive operations were undertaken for at least six hours each operator day.

Terminology for life-history stages in white sharks (young-of-the-year, juvenile, sub-adult, adult) follow the length-based definitions of Bruce and Bradford (2012).

### Sea surface temperature data

Daily sea surface temperature (SST) data for a 0.5 degree square centred on North Neptune Island were extracted from CSIRO’s Spatial Dynamics Ocean Data Explorer (SDODE) product series as a quality controlled (cloud pollution removed) composite including night and day Advanced Very High Resolution Radiometry (AVHRR) data (Hartog *et al.* 2013). Mean SST was calculated for each month of the 14 year time series (January 2000 to December 2013) from these daily data.

### Analyses

Sex ratios were compared between individual months via a paired *t*-test; Chi-square ($\chi^2$) analysis was used to compare overall sex ratio data. Statistical significance was determined at $p = 0.05$. Statistical analyses were performed using R statistical software version 3.1.1 (R Development Core Team, 2014).

## Results

### Sex ratio

The daily mean number of males sighted at the Neptune Islands by month was significantly higher than females (paired *t*-test; df 156; $t$=9.39 $p$ <0.0001) with males on average outnumbering females by 3.2:1 over the entire period of the study ($\chi^2$= 1327.2; $p$>0.0001). Both males and females showed some degree of seasonal variation in abundance which was most pronounced in females (Figure 2). Females showed a clear annual trend, with a peak in abundance between May and August each year (usually in June) with the exception of years 2001 to 2003. In 2001 and 2002, female abundance peaked earlier, in April; females were almost entirely absent from the Neptune Islands during 2003 with very low numbers recorded in January. Relatively low numbers were also observed during 2004, although the timing of occurrence conformed to the expected May-August peak in abundance (Figure 3). Males were encountered throughout the year. Males were generally lowest in abundance in March and gradually increased in abundance over the remainder of the year (Figure 2), with numbers generally peaking from December to February. Males were also recorded in low abundance throughout 2003 (Figures 3 + 4).

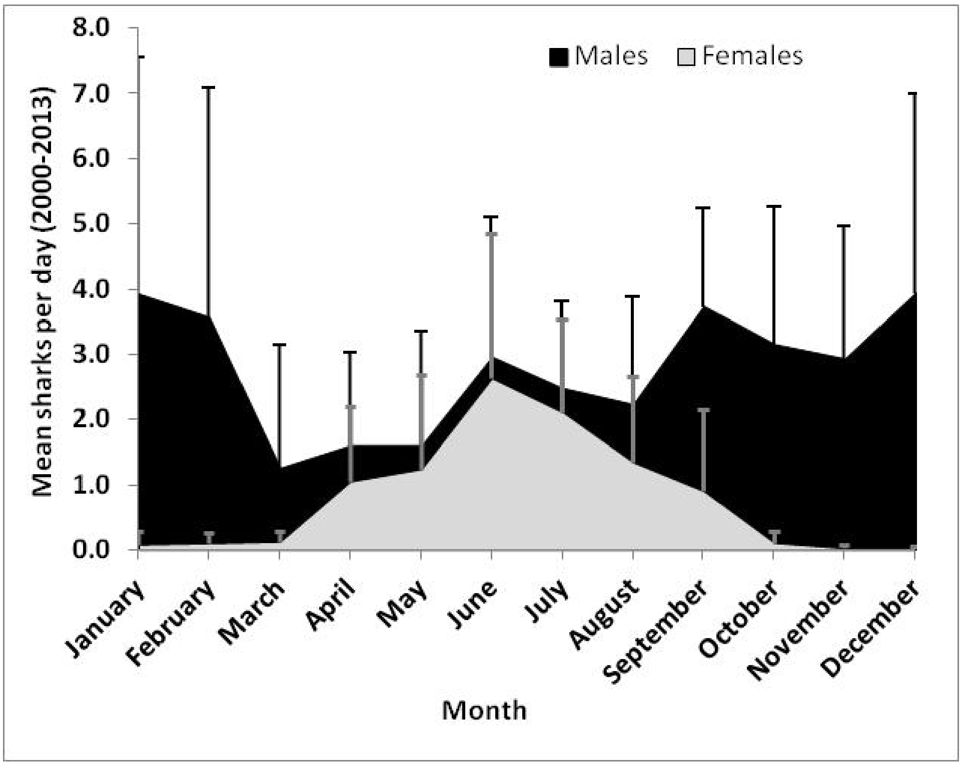

Figure 2: Average monthly abundance of male and female sharks at the North Neptune Islands 2000 – 2013). Vertical bars represent one standard deviation of the mean.

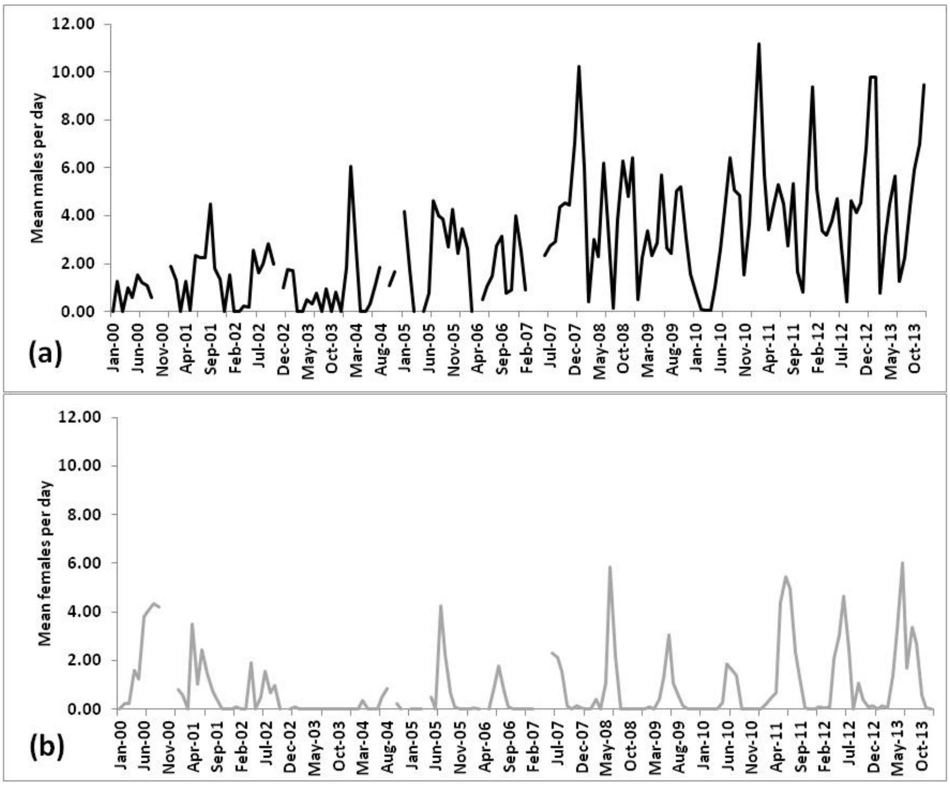

Figure 3: Monthly mean number of sharks sighted per day; January 2000 - December 2013: a) males, b) females. Gaps indicate months where no data were collected (i.e. no where SCDO trips were undertaken).

The number of females present during their peak season of occurrence each year was significantly correlated to the number of males during the same period (Figures 4 + 5; $r^2 = 0.69$). However, overall during these periods there was a trend towards a greater number of males than females (2000-2013:

males mean = 2.27; females mean = 1.93) although the difference was not significant (paired *t*-test $t = -1.436$ $p = 0.17$).

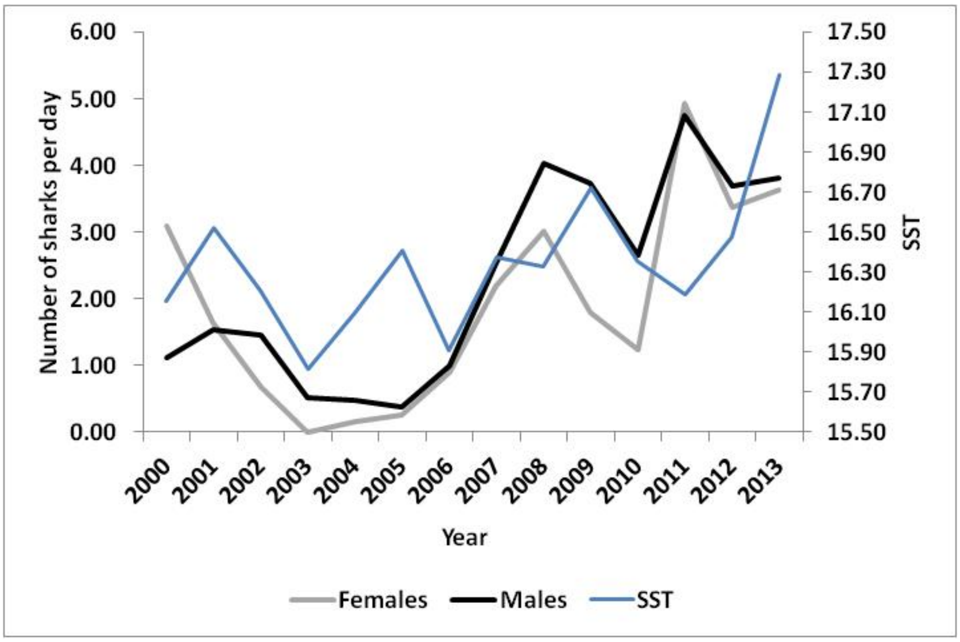

Figure 4: Seasonal peak in female white shark abundance (mean for May – July) at the Neptune Islands for years 2000 to 2013. The average abundance of males and the mean SST is also shown for the corresponding three month period each year.

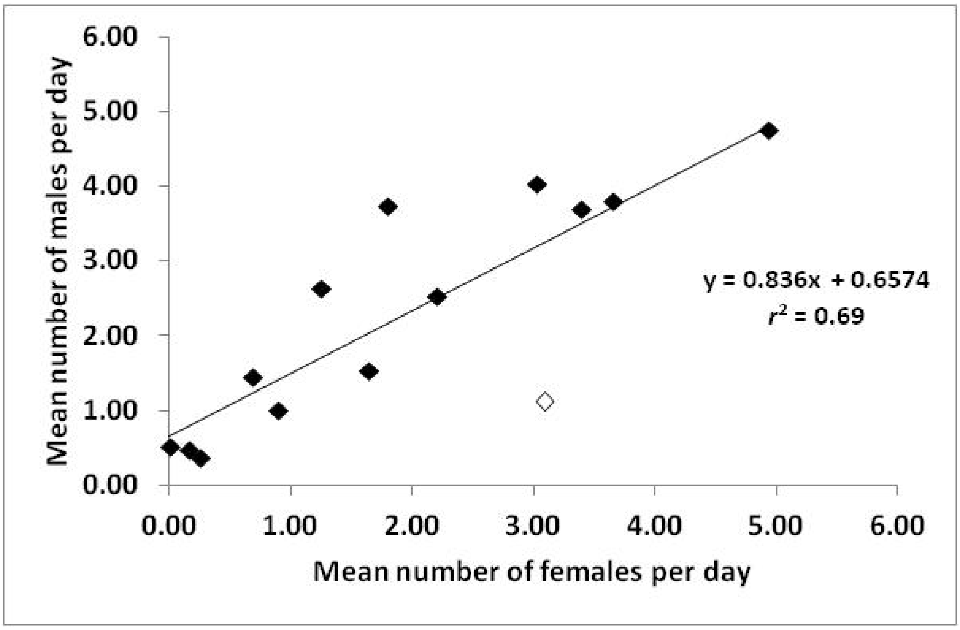

Figure 5: Relationship between the mean seasonal numbers of female white sharks sighted in May to July each year and the numbers of males sighted over the same period (2000 to 2013). The year 2000 (open diamond) recorded an anomalously low number of males. It is possible that this was due to errors in scoring juvenile males in the first full year of log-book records. Removal of this outlier increases the $r^2$ to 0.85.

## Estimated lengths

Estimated lengths were only consistently recorded from January 2011, after logbooks were redesigned to incorporate these data. Estimated lengths (January 2011 to December 2013) ranged from 1.4 to 5.6 m, with the majority of sharks (68%) ranging from 3.0–4.5 m (Figure 6). Adult females (total length ≥ 5.0 m) were relatively rarely encountered, comprising only 2.7% of sharks recorded. The mean length for females was significantly higher than males in 2012 but there were no significant differences in the mean lengths between sexes in either 2011 or 2013 (Table 1).

Table 1: Comparison of male and female sizes between years (2011-2013). Unpaired t-test assuming unequal variances; bold indicates significant *p* value.

| Year | Mean length (est. TL in metres) | | *t* (*p*) |
|---|---|---|---|
| | Females (range) | Males (range) | |
| 2011 | 3.8 (2.0 – 5.5) | 3.8 (2.0 – 5.0) | 1.921 (*p* = 0.055) |
| 2012 | 4.1 (1.4 – 5.6) | 3.8 (1.5 – 5.0) | **5.028 (*p* < 0.0001)** |
| 2013 | 4.0 (2.0 – 5.6) | 3.9 (2.0 – 5.0) | 0.476 (*p* = 0.634) |

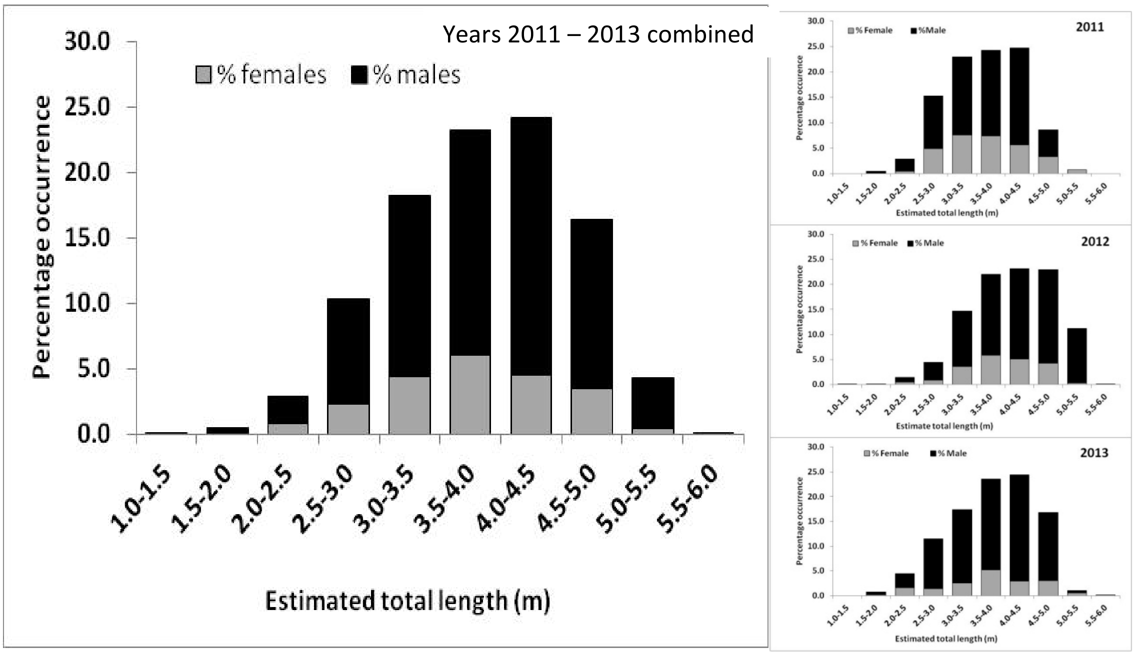

Figure 6: Length distribution of sharks sighted at the Neptune Islands (2011 – 2013).

Very few young-of-the-year sharks were recorded, and it is possible that the length of these sharks was underestimated. Females of all three remaining life-history stages (juvenile, sub-adult, adult) were present during each annual period of peak abundance during 2011, 2012 and 2013. In contrast to the long-term (2000–2013) average, males were least abundant in August during these three years. However, males of all life-history stages were encountered in similar proportions throughout the year (Figure 7).

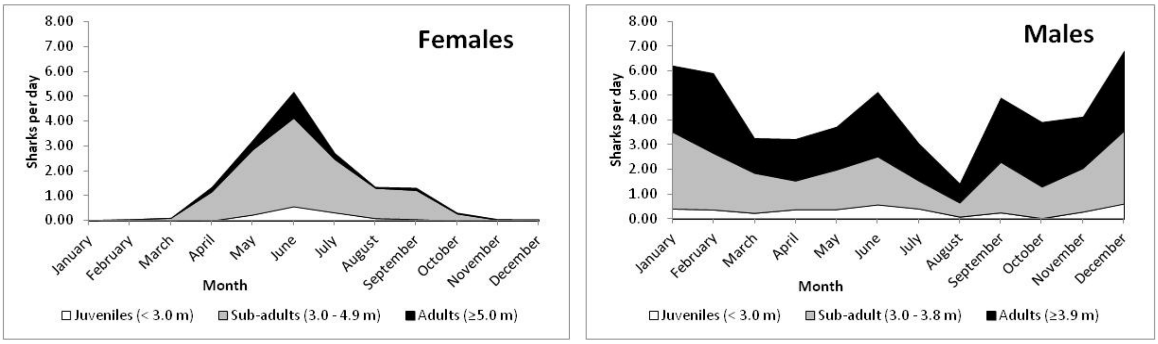

Figure 7: Average numbers of sharks by sex and life-history stage observed at the North Neptune Islands (2011 – 2013).

## Sea surface temperature

Average monthly sea surface temperatures in waters surrounding the Neptune Islands showed a clear annual cycle with the highest temperatures in January-February (19.60–19.85 °C) and lowest temperatures in August-September (14.96–15.07 °C). Stand-out years were the above average temperatures for most of 2013 and the below average temperatures for most of 2003 (Figure 8). During the peak annual season for females, mean temperatures ranged from 15.82 °C in 2003 to 17.29 °C in 2013. Mean sea surface temperature was inter-annually variable during this period but showed an overall increasing trend from 2003 to 2013 (Figure 4).

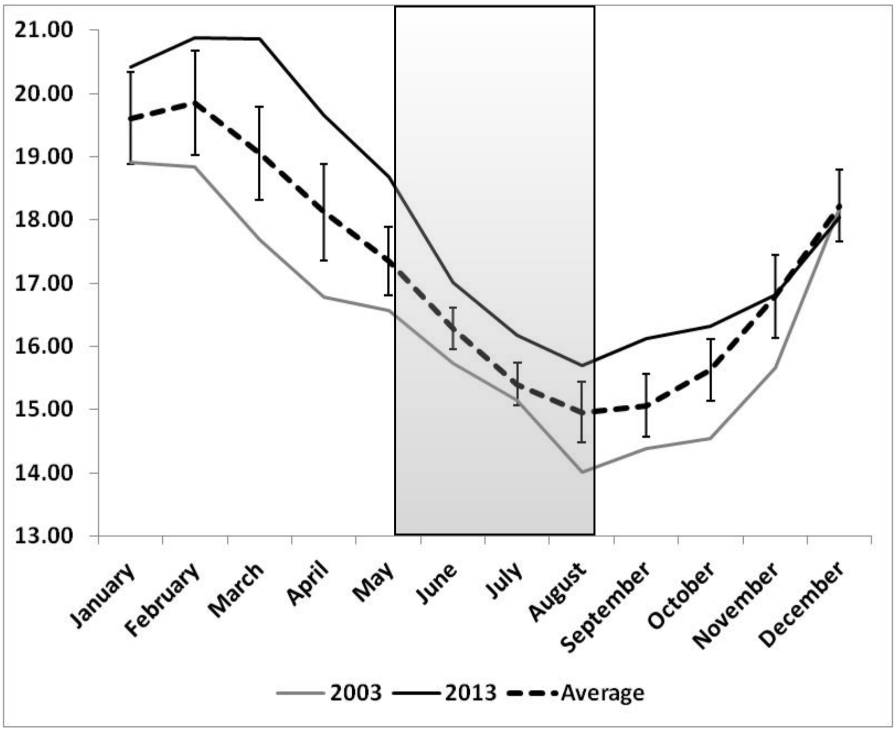

Figure 8: Mean monthly sea surface temperature cycle at the North Neptune Islands (2000 – 2013). Bold dashed line indicates the average over all 14 years; error bars +/- 1 standard deviation; solid lines indicate the stand-out warm and cool years of 2013 and 2003 respectively. Shaded area indicates the period when female sharks are present.

## Discussion

We identified consistent annual patterns in the presence of female white sharks at the Neptune Islands in South Australia during autumn-winter, based on 14 years of data, which differed from the year-round pattern of visits by males. The overall pattern of occurrence by male and female white sharks at the Neptune Islands was initially described by Robbins (2007) and these same data were later re-examined by Robbins and Booth (2012). Their data spanned the years 2001 to 2004 during what appears now, based on our longer term record, to be an anomalous period where overall shark abundance (both sexes) at the Neptune Islands was low, particularly in 2003. Their analyses were also limited by a lack of observations during summer periods. Despite these limitations, these studies provide various observations consistent with our longer term record. Specifically, these authors reported an overall sex ratio dominated by males (3:1) similar to our observed long-term record of 3.4:1, a peak in female abundance in June, a low overall number of adult females (2.4% of sharks recorded compared to our 2.7%), males present in nearly every month and an increase in the abundance of males towards spring and summer.

Our long-term data thus support Robbins (2007) and previous observations by Strong *et al*. (1992) that the North Neptune Islands is a male dominated site for white sharks during much of the year. Our data indicate that males continue to arrive at, and depart, this site throughout the year. However, individuals are only temporary visitors with periods of individual residency ranging from 1 to 92 days (median 11 d, Bruce and Bradford 2013). Some sharks show a propensity for consistent annual visits while others show a less structured and more frequent visiting regime (Bruce *et al*. 2005, Bruce and Bradford 2013). The average abundance of males varies by month and between years, but is generally lowest in March after which it then generally increases towards a summer peak in December–January. Despite this seasonal cycle in the abundance of males, the relative proportions of adult, sub-adult and juveniles were evenly distributed throughout the year. Male sharks showed no propensity for a size-based pattern in their seasonal timing of visits. There was a seasonal influx of females during late autumn and winter each year (except for the years 2001 to 2003), with a peak in abundance usually in June. Similar to males, females of all life-history stages visit during this well defined autumn-winter period. Robbins and Booth (2012) suggested that the presence of adult females during autumn-winter may exclude males during this period. However, our data indicates that the number of adult females recorded at the Neptune Islands is extremely low; male and female sharks of all life-history stages are present during the autumn-winter and that males are present in similar or slightly higher numbers to females during this period. Furthermore, we found that the number of males present during the autumn-winter varied between years but was significantly positively correlated with the number of females. This indicates that interannual variations in abundance are similarly reflected in both males and females during this period. Thus we found a consistent annual pattern of a seasonal influx of females (of all sizes) regardless of the presence of males (of all sizes) and no evidence in the longer-term record of segregation by size, nor exclusion of males by the presence of females at this site. This is consistent with previous findings by Strong *et al*. (1992) of an overall lack of size-based segregation in white sharks at both North Neptune Island and Dangerous Reef (an Australian sea-lion colony in lower Spencer Gulf) during the early 1990s.

The observed seasonal of occurrence by female white sharks at the Neptune Islands is not consistent with predictions from a ‘thermal-niche’ hypothesis. This hypothesis leads to the prediction that female sharks seek out warmer waters than male conspecifics in order to increase their metabolic rate, thereby enabling more rapid growth, or in the case of pregnancy, an increase in the developmental rate of embryos (Wearmouth and Sims 2008). Support for this hypothesis in sharks was indicated by Economaks and Lobel (1998) who reported that pregnant grey reef sharks (*Carcharhinus amblyrhynchos*) segregated from male conspecifics in the warmer waters of atoll lagoons. Robbins and Booth (2012) concluded that female white sharks were more frequently observed than males at the Neptune Islands during warmer water temperatures and the cooler conditions of 2003 resulted in an absence of females visiting during that year. This led them to speculate that females may favour warmer waters to promote and accelerate embryonic development of young as a result of comparatively increased internal core body temperatures. However, our data indicate that female white sharks increase in abundance at the Neptune Islands from April through to June-July when mean water temperatures are rapidly declining and, by July, are close to their August-September minimum of approximately 15.0 $^{o}$C. In addition, most visiting females were juveniles and sub-adults. The number of adult females was extremely low and females were almost entirely absent during the warmer months. Females, including the few adults recorded, were thus present towards the coolest, rather than the warmest, time of the year. Males, however, visited throughout the year including during early to mid-summer when water temperatures were 18.2 – 19.6 $^{o}$C and close to their seasonal peak. While it is possible that female white sharks, when pregnant, may seek out warmer waters to increase the developmental rate of their embryonic young as proposed by Robbins and Booth (2012), this would appear not to be the reason why female white sharks of all life-history stages visit the Neptune Islands over a highly focused period during the autumn-winter. In addition, the requirement to seek out such a thermal niche would presumably be more likely to apply to ectothermal species of sharks. White sharks are known endotherms (Goldman 1997) and thus their behaviour and distribution is less likely to be directly influenced by thermal cues. However, Domeier and Nasby Lucas (2012) noted that tagged adult female white sharks remained in areas of significantly higher SST when in offshore waters compared to males that returned annually to coastal aggregation sites, although interpretations were confounded by females also spending considerable time in cooler waters at depth during these periods. Similarly, Klimley (1985) noted that adult female white sharks were more common in warmer waters to the south of Point Conception off California. Thus although a preference for warmer temperatures by females cannot be ruled out, it fails to explain their seasonal presence at the Neptune Islands and suggests a more complex interplay of factors or a more specific requirement that draws females to this site during the autumn-winter period.

The Neptune Islands hold some of the largest colonies of New Zealand fur seals (*Arctocephalus forsteri*) found in Australian waters, with pup production in 2014 estimated at approximately 7,900 and accounting for 38% of the entire South Australian population (Shaughnessy *et al*. 2014). Despite their name, the New Zealand fur seal is endemic to both Australia and New Zealand and is one of several otariid species world-wide which are common prey for white sharks. The highly seasonal presence of female sharks at the North Neptune Islands over the 14 year period of this study is consistent with a pattern that would maximize predation on adult female fur seals and pups as surmised by Robbins (2007). Pupping is centred in mid-December (Page *et al.* 2005). Lactating female seals resume foraging activities within a week or so of pupping, but do not establish regular foraging periods until April (Stirling 1971) coinciding with the arrival of female white sharks at the Neptune Islands. New Zealand fur seal pups increase their in-water activity over ensuing months gradually venturing into near-shore waters around such colonies prior to weaning (Baylis *et al*. 2005, Bradshaw *et al.* 1999). Some seal pups have commenced weaning by August, after which the numbers of pups and female seals decline as they depart the colony. Median pup weaning date is early October with weaning largely complete by November when most pups and female seals have departed (Goldsworthy 2006). Similarly, female white sharks show an increase in average abundance from April through to a peak in June-July and then decline in abundance through August-September as pups commence weaning, with all female sharks having departed by October-November after pup-weaning is complete. This indicates that female sharks are most abundant at the Neptune Islands immediately prior to the weaning of pups when the numbers of female seals and pups in waters close to the colony are likely to be highest.

There is consistent evidence for a focused pattern of seasonal visits by female white sharks at otariid seal colonies worldwide, as is predation on seal pups. Based on pop-off satellite tag data, Domeier and Nasby-Lucas (2008) noted that the appearance of male white sharks at Guadalupe Island coincided with the period of summer pupping in the Guadalupe Island fur seal, but that females generally arrived at a ‘later time’. These authors report that sharks generally departed Guadalupe Island in winter-spring, coinciding with weaning in seal pups (Pierson 1978). Domeier and Nasby-Lucas (2008) also noted that the span of departure dates observed was much greater for males than females. This pattern, although less complete than our data-set, is consistent with our observations at the Neptune Islands of an extended period of occurrence by male sharks and a more focused seasonal appearance of females.

Martin *et al.* (2005) and Laroche *et al.* (2008) noted that predation by whites sharks on Cape fur seal pups at Seal Island, in False Bay, South Africa was significantly higher than on any other age-classes. Based on acoustic tagging data, Kock *et al.* (2013) recorded an autumn-winter peak in female white sharks (1.7 to 5.0 m TL) around Seal Island and made similar observations that sharks fed predominantly on young-of-the-year seals. Male sharks similarly peaked in abundance during the autumn-winter, but visits by males to Seal Island were recorded throughout the year. Sharks, in general, departed Seal Island coinciding with the weaning of pups. These observations again suggest a focus by female sharks during the pre-weaning period for seal pups at Seal Island, and a lack of segregation by size and sex, specifically when sharks aggregate around the seal colony. In this case, however, the peak abundance of male sharks at this site suggests they too may primarily take advantage of the availability of pups at this time.

Our long-term data suggest that female sharks preferentially target specific life-history stages of seals at the Neptune Islands on an annual basis and studies world-wide suggest that such behaviour may be widespread in the species. Our conclusions provide an explanation to the question posed by Domeier and Nasby-Lucas (2008) as to ‘why female white sharks might delay their arrival at Guadalupe Island compared to males’, if in doing so female sharks ensured that their presence at the island coincided with the peak period in near-shore availability of pre-weaning pups and lactating adult female fur seals.

If this pattern of occurrence at the Neptune Islands is a strategy by female white sharks to optimise predation on adult female fur seals and pups, then the same cannot necessarily be concluded for all male sharks. The Neptune Islands continue to receive visits by male sharks throughout the year and they show an overall December-January peak in abundance when female sharks are absent. This may indicate a greater level of dietary selection and hence a different annual regime of foraging strategies by female white sharks relative to many, if not all, male conspecifics.

Sex-specific foraging behaviour is widespread in marine vertebrates, particularly in fin-fish (Wearmouth and Sims 2008) and has been specifically identified in sharks. McCord and Campana (2003) reported differences between the sexes in the diet of blue sharks, *Prionace glauca*, resulting from sex-specific preferences in foraging locations. Klimley (1987) suggested that female hammerhead sharks adopt an offshore foraging strategy earlier than males to maximise their growth rates. This would ensure an equivalent reproductive output between the sexes where females need to reach a larger size prior to reproduction. Such observations have led to the development of the 'forage-selection' hypothesis to account for observed patterns in sexual segregation. This hypothesis focuses on differences in nutritional requirements between sexes that generate different foraging strategies and thus the occupancy of different habitats in space and/or time. Predictions from this hypothesis would be for female sharks to seek out different prey, or consume higher quantities of prey and show a more rapid growth rate than males. Female white sharks mature at a larger size than males (Francis 1996, Pratt 1996) and various aging studies suggest a more rapid growth rate in females (Hamady *et al*. 2014, Tanaka *et al*. 2011). Sex-specific foraging strategies have not been demonstrated in white sharks although Kock *et al.* (2013) found an almost exclusive inshore occurrence of females and an absence of males in False Bay, South Africa during periods when the abundances of finfish and other elasmobranch species are high. These observations suggest that sex-specific foraging strategies may exist. The near year-round visits by male white sharks to the Neptune Islands may represent a strategy whereby males continue to exploit the high quality resource in the form of seals, resident finfish and other sharks throughout the year whereas females seasonally target the more abundant and perhaps energetically less demanding predation of seal pups. This would be in-line with predictions from the forage selection hypothesis.

The focused seasonal peak in occurrence of female white sharks at the Neptunes Islands and the year-round visits by males, suggests that male and female sharks are likely to show different overall patterns of movements and distribution across southern Australian waters. Thus some form of sexual segregation is likely to be a feature of this population. The different patterns of occurrence of male and female sharks at the Neptunes, however, is not strictly sexual segregation at this site as sexes, when both are present, occur in approximately equal numbers across a range of sizes and life-history stages. The seasonal influx of females may, however, be a product of spatial segregation of sexes at other times of the year that breaks down during the common aggregation period around the Neptune Islands in autumn-winter. This is similar to that reported by Kock *et al.* (2013) who observed white sharks of both sexes aggregating around the Seal Island pinniped colony in False Bay, South Africa, during autumn and winter across sizes ranging from 2.5 to 5.0 m. That study reported marked spatial segregation of the sexes at other times of the year. Domeier and Nasby-Lucas (2006, 2008) also recorded the common occurrence of both male and female white sharks across a range of sizes from 2.4 to 5.2 m around Guadalupe Island pinniped colonies in Mexico during summer. A following study found marked differences between males and females in the spatial extent of movement and areas occupied during periods when sharks were absent from Guadalupe Island (Domeier and Nasby-Lucas 2012). Duffy *et al.* (2012 – citing Duffy 'unpublished data') similarly reported a lack of size or sexual segregation in white sharks visiting New Zealand pinniped colonies. Combined aggregation of the sexes across a range of sizes thus appears to be widespread in white sharks that seasonally visit pinniped colonies with mounting evidence for sexual segregation at other times of the year.

Differences in movement patterns and areas occupied by males and females have not yet been explored for white sharks in Australia. However, geographic segregation of sexes was reported by Bruce (1992) and Strong *et al*. (1992, 1996) in the South Australian region with 'inshore islands' (i.e. those within southern Spencer Gulf) showing a sex ratio strongly favouring females and the latter studies identifying the Neptune Islands as being dominated by males. Strong *et al*. (1996) also reported that the sex ratio observed at Dangerous Reef, one of their study's 'inshore islands' with a female-bias observed during summer, may change temporally as previous anecdotal reports by recreational fishers and documentary makers had sighted primarily males during this time of year. An explanation for such a temporally variable sex ratio may be if female white sharks similarly targeted peak otariid pre-weaning periods at this site. Dangerous Reef holds Australia's largest colony of Australian sea-lions (*Neophoca cinerea*), Goldsworthy *et al.* (2010). Unlike the annual breeding cycle of New Zealand fur seals, Australian sea-lions have a 17-18 month breeding cycle (Gales *et al*. 1994) meaning that pupping alternates between summer and winter periods and thus the seasonal availability of pre-weaning pups also alternates between seasons over this cycle. If female sharks only targeted the pre-weaning period in this species it would be reflected in a temporally variable sex ratio that alternated between summer and winter pupping seasons.

## Conclusion

We found consistent patterns in the seasonal presence of white sharks at the Neptune Islands in South Australia over 14 years that suggest females seasonally aggregate in late autumn and winter coinciding with the maximum in-water availability of lactating female New Zealand seals and seal pups. Although male sharks occurred in approximately equal numbers to females during this period, males also visited throughout the year and their overall abundance generally peaked during summer when females were absent. The differences in female and male patterns at the Neptune Islands suggest that foraging strategies/prey selection differ between sexes in white sharks across the life-history stages represented. Although segregation by sex and size was not strictly evidenced at the Neptunes, the highly focused seasonal pattern of occurrence by females compared to the year-round visits by males suggests that there are likely to be differences between the sexes in overall distribution and movements patterns across southern Australia. This may lead to spatial segregation of the sexes outside of the autumn-winter period throughout the region. Our data suggest that sex-specific foraging strategies may play an important role in structuring movement patterns in white sharks. Differences between sexes in distribution, movement patterns and foraging strategies are likely to have implications for modelling the consequences of fisheries by-catch between regions or jurisdictions and other spatially or temporally discrete anthropogenic impacts on white shark populations. Such differences would also suggest a need to treat the sexes separately in population and movement models as well as under recovery plan actions.

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