Cape fur seals (*Arctocephalus pusillus pusillus*) adjust traversing behaviour with lunar conditions in the high white shark (*Carcharodon carcharias*) density waters of Mossel Bay, South Africa

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"CAPE FUR SEALS ADJUST TRAVERSING BEHAVIOUR WITH LUNAR CYCLE"

ABSTRACT

White sharks (*Carcharodon carcharias*) are highly visual predators, leading to the hypothesis that the predation risk for foraging Cape fur seals (*Arctocephalus pusillus pusillus*) might differ with ambient light conditions. This study investigated the relationship between environmental fluctuations of ambient light and the traversing behaviour of Cape fur seals in and out of their colony at Mossel Bay, South Africa to better describe potential predator avoidance strategies. A total of 12,144 traversing events were observed over a four-year period and there was an overall trend for Cape fur seals to traverse less often but in relatively larger group sizes during periods when white sharks are suggested to be more active. Specifically, Cape fur seal activity was reduced during winter when white sharks are most actively hunting, and most traversing behaviour occurred at night when Cape fur seals were less likely to be detected by white sharks. However, among nocturnal observations Cape fur seal group sizes increased significantly with moonlight. Although nocturnal predations of Cape fur seals by white sharks have been observed before in Mossel Bay, this is the first study to indicate Cape fur seals might respond to the increased risk of improved white shark visual acuity during moonlit nights by seeking safety in numbers while foraging. Further investigations are needed to assess the effect of the lunar cycle on white shark nocturnal hunting behaviour, but observations presented here suggest that white sharks may pose a bigger threat to Cape fur seals under the light of a full moon.

KEY WORDS

Predator avoidance; Pinniped; Lunar cycle; Safety in numbers; Mobbing; Predator-prey

INTRODUCTION

The threat of predation often prompts a behavioural response in prey, which may help to minimise its risk of predation (Brown et al. 1999). Such changes in behaviour may involve avoiding habitats or areas with increased risk of predation (Kotler et al. 1991; Brown & Kotler 2004) or relying on strategies such as grouping (Hamilton 1971; Hager & Helfman 1991; Viscido et al. 2001). Prey may also respond to predation risk by temporally shifting activity to a safer period, such as times when predators are less active or not present (Lima & Bednekoff 1999; Turner & Montgomery 2003; Brown & Kotler 2004). It has been suggested that Cape fur seals (*Arctocephalus pusillus pusillus*) employ all three of the above strategies to avoid predation from patrolling white sharks (*Carcharodon carcharias*) while traversing between their colonies and their offshore feeding grounds (Hammerschlag et al. 2006; Laroche et al. 2008; Johnson et al. 2009b). Cape fur seals typically colonise small, rocky, offshore islands as well as mainland sites along the southern African coastline (David et al. 1986). During the summer months (December to February) females typically give birth to one pup, which is subsequently nursed on land for a period of eight to ten months, punctuated by female foraging trips to sea (David et al. 1986). Lactating female seals spend substantial periods of time traversing between their colony and offshore feeding areas relative to nonbreeding females, and may spend up to a week foraging out at sea (David et al. 1986; Gamel et al. 2005). Cape fur seal pups first begin to enter the water during the late autumn and winter months (May to August; David et al. 1986), and during these periods of heightened foraging behaviour of lactating females and naïve pups entering the water for the first time, white sharks are consistently patrolling inshore waters, particularly within a few hundred metres of Cape fur seal colonies (Martin et al. 2005; Hammerschlag et al. 2006; Laroche et al. 2008). To avoid predation during foraging trips, Cape fur seals have been reported to use predator avoidance strategies such as grouping (safety in numbers), and diving to avoid vulnerability at the surface (Laroche et al. 2008), as well as mobbing behaviour (Johnson et al. 2009b). It has also been suggested that Cape fur seals may limit their traversing periods to particular times of day when ambient light conditions might reduce their risk of being predated (Hammerschlag et al. 2006; Laroche et al. 2008).

Previous studies have shown that white sharks may be more active in predating seals during early daylight hours and low light conditions such as crepuscular periods (Martin et al. 2005; Hammerschlag et al. 2006; Johnson et al. 2009a; Martin & Hammerschlag 2012). During crepuscular periods sharks might have a visual advantage over their prey by remaining undetected due to poor light penetration through the water, whilst enough light is available for sharks to observe pinnipeds porpoising at the surface (Laroche et al. 2008; Martin & Hammerschlag 2012). Despite this, white sharks are reported to have a 4:1 rod to cone ratio in their retinas (Gruber 1975), one of the lowest among studied sharks (Collin 2018), suggesting that they might have very poor night vision. This prediction is partially supported by studies in False Bay, South Africa where Cape fur seals were observed to predominantly traverse to and from their colonies at night-time when it is thought to be too dark for white sharks to detect them effectively (Hammerschlag et al. 2006; Laroche et al. 2008). However, reports from Año Neuvo, USA (Klimley et al. 2001) as well as recent observations in Mossel Bay, South Africa (R. Johnson unpublished data) suggest that white sharks are able to nocturnally hunt pinnipeds as long as a minimal source of light exists from above, such as the presence of anthropogenic light or moonlight. In addition to this, juvenile white sharks have been reported to dive deeper on nights with a full moon, suggesting that their hunting behaviour may be affected by the lunar cycle (see Collin 2018).

Coinciding with the above patterns of shark activity, colonies of Galapagos fur seals (*A. galapagoensis*) have been observed to be more likely to stay onshore during full moon phases (Trillmich & Mohren 1981; Horning & Trillmich 1999). Two possible hypotheses (Trillmich & Mohren 1981) were suggested to explain this pattern: 1) anti-predator behaviour, and 2) decreased offshore foraging efficiency due to the effect of moonlight on the vertical migration of their prey in the water column. Although a traversing seal on the water's surface may be silhouetted against a full moon-lit sky thereby increasing its chances of being predated upon (Hammerschlag et al. 2006), the possibility that Galapagos fur seals avoid traversing during moonlit nights due to predator avoidance was ruled out by Horning and Trillmich (1999). This was primarily because during their study Galapagos fur seals showed no decrease in activity during dawn and dusk periods when predation risk was highest. Currently, no studies have yet investigated the effects of the lunar cycle on nocturnal traversing behaviour in Cape fur seals. However, a recent assessment of white shark predatory behaviour in False Bay indicates that white sharks have a reduced likelihood of successfully predating a Cape fur seal during dawn hours when the moon is full (Fallows et al. 2016). These authors hypothesised that although moonlight might increase predation risk for Cape fur seals at night, the added illumination from a full moon at dawn could also work to the Cape fur seals' advantage by enabling them to see white sharks lurking deeper below in the water column.

The current study investigated the relationship between environmental fluctuations of ambient light, such as time of day and lunar cycle, and the traversing behaviour of Cape fur seals to and from an island colony in high white shark density waters off of Mossel Bay, South Africa. It was hypothesised that Cape fur seals might adjust the frequency of their traversing events and group sizes around ambient light conditions to minimise the chance of predation by white sharks. Therefore this study aimed to identify how Cape fur seal traversing frequency and group size covaried with a) time of day, b) season and c) lunar phase. These behaviours were then compared to previously established patterns of temporal variation in white shark hunting activity, enabling greater insight to the relationship between this predator and its prey in South African waters.

METHODS

Study Site

The study was conducted in the coastal waters surrounding Seal Island, approximately 800m offshore from Mossel Bay's Dias beach (34º08´S, 22º07´E) on the southern coastline of South Africa. The island is a popular annual haul-out site for Cape fur seals colonised by over 4,000 individuals and classified as a breeding colony (Wickens et al. 1991). The bay is an aggregation area for white sharks, which are often observed patrolling the waters surrounding Seal Island, especially in winter months (Johnson et al. 2009a). As it was not possible to simultaneously monitor all sides of the island, all observations in this study were made within a single section, referred to as 'sector 2' (R. Johnson unpublished data; Figure 1). Pilot studies indicated that > 90 % of Cape fur seal groups departed from and ~ 50 % of groups returned through this section of the island (R. Johnson unpublished data).

Insert Figure 1 about here

Field Observations

From July 2008 to December 2011 a total of 69 surveys of Cape fur seal movements to and from Seal Island were conducted (Table 1). Forty of these surveys each lasted 24 hours, while the other 29 surveys entailed two to 23 hours of observations over haphazardly selected hours of the day. It total, cape fur seal movements were observed for 1,251 hours and 32 minutes over the four-year period (Table 1). From 2008 – 2010, daytime observations were conducted from the top of a 13-story hotel located on Dias Beach, approximately 1 km from and overlooking Seal Island (Fig 1). From this vantage point all seal movement around the Island was visible. From sunset, observations from the hotel roof were no longer possible, so additional observations were made from a vessel anchored approximately 150 m off Seal Island in sector 2 (Fig 1). In 2011, observations from the top of the hotel were discontinued and all observations were made from a vessel anchored in the same location as described above. Therefore, all dawn, dusk and night-time surveys were observed from the same research vessel, however daytime observations were recorded from two different locations depending on the year of the survey (Table 1), and this was considered during analyses (see below).

During surveys, observations were recorded by a pair of researchers. As this pair changed with each survey, all researchers underwent rigorous training with the principal investigator to minimise inter-observer bias. For consistency, a traversing event was logged when an individual seal or group of seals traversed past the anchored boat (or 150 m marker). Cape fur seal movements were not monitored once they were further than 150 m from the island, but to the observers' knowledge there were no cases of Cape fur seals immediately turning back after traversing past this point. For each traversing event, the time and direction of the group (departing or returning to Seal Island) were recorded. The size of each group was recorded as one of seven group size categories (1, 2, 3 - 5, 6 - 9, 10 - 15, 16 - 24, 25 +). White sharks were not the focus of these surveys and so their behaviours were not intentionally observed, nor recorded in a standardised manner. However, any white shark predations of Cape fur seals observed these during surveys were included in the results as qualitative anecdotes.

Insert Table 1 about here

Categorisation of Environmental Data

The time of sunrise and sunset, as well as the proportion of moon face illuminated (MFI) were obtained for each date of survey from the United States Naval Observatory (USNO; www.usno.navy.mil/). Time of day was split into four periods (dawn, day, dusk and night). For the purposes of this study, dawn was defined as one hour preceding and one hour following sunrise, and dusk was defined as one hour preceding and one hour following sunset. Day was defined as the period between dawn and dusk, and night as the period between dusk and dawn. The duration (in minutes) of each period during each of the 69 surveys was recorded in order to convert traversing frequencies to rates. Time of year was split into four seasons: summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). The distribution of MFI values were normalised using an arcsin transformation, and these values were used to represent lunar conditions for each date of survey.

Statistical Analyses

The effects of environmental conditions on the frequency of Cape fur seal groups traversing to and from Seal Island were analysed using mixed-effects Poisson regressions in R version 3.3.1 (R Core Team 2013). To do this, the total numbers of groups both departing and returning to the island were calculated for each period of day within every survey. Then the frequencies of departing and returning groups were each analysed separately, using the 'glmer' function in the 'lme4' R package. Within these formulae, model families were set to 'Poisson' and response variables were offset by a natural log of the observation time. To account for variance in observations potentially resulting from having two observation points (hotel and boat), 'Year' was used as an unordered random factor and 'Observation point' was included with the other fixed factors as a blocking variable. The environmental variables included in the formulae as fixed factors were: time of year ('season'), time of day ('period') and arcsin transformed MFI ('moon'). Interactions among fixed factors were checked for significance and removed from formulae if not significant.

The variances in size of Cape fur seal groups departing and returning to Seal Island were analysed using mixed-effects ordinal logistic regressions. To do this, the raw data were used, and the size classes of Cape fur seal groups during all traversing events were analysed as ordered factor response variables with the 'clmm' function in the 'ordinal' R package. Both 'year' and 'survey' were included in formulae as unordered random factors in order to account for inter-observer bias and differing observation points among surveys. The environmental variables: ‘season’, ‘period’ and ‘moon’ were included as fixed factors. As before, insignificant interactions were removed from formulae.

RESULTS

Diel and Seasonal Variation in Traversing Frequency

Frequencies of traversing Cape fur seal groups varied significantly with time of day (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 1{,}092.88$, $P < 0.001$; and returning groups: $\chi^2_3 = 1{,}575.144$, $P < 0.001$). Traversing behaviour both to and from Seal Island was significantly reduced during the day compared to other time periods ($P < 0.001$; Figure 2). Cape fur seals were observed to predominantly depart Seal Island during dusk periods, and the majority of groups observed during dawn periods were returning to the island (Figure 2). Cape fur seals were observed to both depart and return to Seal Island in relatively high frequencies during night-time (Figure 2).

Season also had a significant effect on the frequency of Cape fur seal groups departing and returning to Seal Island (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 135.27$, $P < 0.001$; and returning groups: $\chi^2_3 = 464.89$, $P < 0.001$). Overall, traversing behaviour both to and from Seal Island was less frequent during winter months (mean groups departing per hour = 4.352 ± 0.545 S.E.; mean groups returning per hour = 2.939 ± 0.519 S.E.; Figure 2). Cape fur seals departed and returned to Seal Island in the highest frequencies during autumn and spring (mean groups departing per hour in autumn = 4.794 ± 0.597 S.E.; and spring = 6.48 ± 0.817 S.E.; mean groups returning per hour in autumn = 5.689 ± 0.809 S.E.; and spring = 4.629 ± 0.689 S.E.; Figure 2). There was a significant interaction between the effects of season and diel period affecting traversing frequency of both departing (likelihood ratio test of mixed-effect Poisson regressions: $\chi^2_9 = 91.82$, $P < 0.001$) and returning groups (likelihood ratio test of mixed-effect Poisson regressions: $\chi^2_9 = 65.644$, $P < 0.001$; Figure 2). Among dawn periods there were more groups both departing and returning to the island during spring months than expected, while there were fewer groups returning to Seal Island during winter months than expected (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 19.58$, $P < 0.001$; and returning groups: $\chi^2_3 = 126.825$, $P < 0.001$). Among day periods there were fewer groups departing Seal Island during winter months than expected (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 8.491$, $P = 0.037$), while season had no significant effect on the frequency of groups returning to the island (mixed-effects Poisson regression for returning groups: $\chi^2_3 = 1.948$, $P = 0.583$). Among dusk periods there were fewer groups observed departing Seal Island during autumn months than expected (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 30.808$, $P < 0.001$), and more groups observed returning to the island during summer and autumn months than expected (mixed-effects Poisson regression for returning groups: $\chi^2_3 = 23.141$, $P < 0.001$). Among night periods, both departing and returning groups were observed in higher frequencies than expected during autumn and spring months, while Cape fur seals were observed to depart and return to Seal Island less frequently at night-time during summer and winter months (mixed-effects Poisson regression for departing groups: $\chi^2_3 = 152.555$, $P < 0.001$; and returning groups: $\chi^2_3 = 389.08$, $P < 0.001$).

Insert Figure 2 about here

Diel and Seasonal Effects on Group Size

Time of day has a significant effect on the size of Cape fur seal groups departing Seal Island (mixed-effects ordinal logistic regression: $\chi^2_3 = 540.92$, $P < 0.001$), but did not significantly impact the size of groups returning to the island (mixed-effects ordinal logistic regression: $\chi^2_3 = 4.546$, $P = 0.208$). Departing groups were most commonly comprised of three to nine individuals during day and dusk periods, and three to five individuals during night periods (Figure 3). Fewer groups departed the island overall during dawn periods, but the size-classes of these groups departed the island during this period in relatively equal frequencies (Figure 3). Returning 'group' sizes were most commonly comprised of single individuals, regardless of the time of day (Figure 3).

Insert Figure 3 about here

Season significantly impacted the size of Cape fur seal groups both departing (mixed-effects ordinal logistic regression: $\chi^2_3 = 11.16$, $P = 0.011$) and returning (mixed-effects ordinal logistic regression: $\chi^2_3 = 8.323$, $P = 0.04$) to Seal Island (Figure 4). Group sizes were statistically the largest during autumn months, when departing group sizes of more than 15 individuals were more common than in other months and individual Cape fur seals returning to Seal Island comprised less than half of observed groups returning (Figure 4). Size class distributions during winter and spring months were statistically similar for both departing and returning groups ($P > 0.1$), but groups tended to be smaller during these seasons than observed during autumn (departing groups sizes in winter: $P = 0.011$; and spring: $P > 0.001$; returning group sizes in winter: $P > 0.035$; and spring: $P > 0.074$; Figure 4). Relative distribution of group size classes for both departing and returning Cape fur seals were smallest during summer, which was the most common season for Cape fur seals to depart Seal Island as individuals (Figure 4). However, due to high variance of observations during summer months this difference was only significant when comparing size classes among returning groups between summer and autumn surveys ($P > 0.02$; Figure 4).

Insert Figure 4 about here

Correlations of the Lunar Cycle and Traversing Behaviour

There was a slight trend for the frequency of Cape fur seal groups departing Seal Island to decrease with MFI, but this pattern was not significant (mixed-effects Poisson regression: $\chi^2_1 = 1.66$, $P = 0.197$). The frequency of returning Cape fur seal groups to Seal Island did significantly decrease with MFI (mixed-effects Poisson regression: $\chi^2_1 = 45.8$, $P < 0.001$), and there was a significant interaction between MFI and time of day impacting the frequency of groups returning to the island (likelihood ratio test of mixed-effect Poisson regressions: χ^2_3 = 9.949, P = 0.019). The negative correlation between MFI and the frequency of Cape fur seal groups returning to Seal Island was the most pronounced during night-time observations (mixed-effects Poisson regression: χ^2_1 = 58.53, P < 0.001; Figure 5). There was no significant interaction between MFI and time of day affecting the frequency of groups departing Seal Island (likelihood ratio test of mixed-effect Poisson regressions: χ^2_3 = 4.214, P = 0.239), and there was no relationship between MFI and the frequency of Cape fur seal groups departing Seal Island during night-time hours (mixed-effects Poisson regression: χ^2_1 = 0.152, P = 0.697).

Insert Figure 5 about here

The size of traversing Cape fur seal groups departing Seal Island did significantly increase with MFI (mixed-effects ordinal logistic regression: χ^2_1 = 11.1, P < 0.001), as did the size of Cape fur seal groups returning to the island (mixed-effects ordinal logistic regression: χ^2_1 = 5.282, P = 0.022). There were significant interactions between MFI and time of day impacting Cape fur seal group size both departing (likelihood ratio test of mixed-effects ordinal logistic regressions: χ^2_3 = 68.315, P < 0.001) and returning (likelihood ratio test of mixed-effects ordinal logistic regressions: χ^2_3 = 15.089, P = 0.002) to Seal Island. The significantly positive relationship between MFI and group size was strongest for departing and returning groups during night-time hours (mixed-effects ordinal logistic regression for departing groups: χ^2_1 = 12.637, P < 0.001; and returning groups: χ^2_1 = 4.449, P = 0.035; Figure 6). In other words, among night-time surveys smaller groups were significantly more likely to be observed departing Seal Island during low moonlight conditions, while larger groups were significantly more likely to be observed departing the island during larger moon phases (Figure 6). This pattern also held true for group sizes returning to Seal Island, although Cape fur seals were very rarely observed returning to the island in groups of ten or more, regardless of moonlight (Figure 6).

Insert Figure 6 about here

Observations of White Shark Predatory Behaviour

Among the 69 surveys observing Cape fur seal traversing behaviour, four predations by white sharks on Cape fur seals were observed (Table 2). One predation occurred during the day, another at dusk on a full moon night, and two other predations occurred during night-time surveys, one of which was during a new moon and the other during a full moon (Table 2).

Insert Table 2 about here

DISCUSSION

Observations reported here indicate that Cape fur seal movement patterns in Mossel Bay covary with time of day, season and lunar cycle. The general observable trend was for Cape fur seals to limit their traversing events and maintain larger group sizes during particular seasonal or diel times corresponding to when predation risk from white sharks might be higher. These times primarily included daytime and crepuscular periods, winter months and moonlit nights. Cape fur seals in this study avoided traversing to and from Seal Island during the day, when increased ambient light may leave them particularly vulnerable to detection by patrolling white sharks. Cape fur seals were began departing Seal Island each evening at dusk, but would typically do so in large group sizes (3 – 15 individuals; Figure 3). Cape fur seals were observed to both come and go during night-time hours, but would do so less often during winter months when white sharks are most active around the island (Ryklief et al. 2014), and they were more likely to traverse in larger groups when more of the moon was illuminated (Figure 6). Cape fur seals were almost never departed Seal Island at dawn, but would rather use this period to return to the island before daylight if they had not done so already.

In comparison with other Cape fur seal colonies along the southern African coastline, these results are similar to observations made in False Bay, where adult Cape fur seals showed a preference for departing during the dark hours between sunset and midnight presumably to minimise the risk of predation by white sharks (Laroche et al. 2008). Cape fur seals at Kleinzee, on South Africa's west coast, have been reported to traverse to and from their colony fairly regularly throughout the day and night (Gamel et al. 2005). However, these authors did observe a peak in Cape fur seal movement during the first few hours following sunrise, which coincided with the daily movement of seals to the water's edge in order to thermoregulate (Gamel et al. 2005). Similar observations were made at the Van Reenen's Bay colony in Namibia, however no night-time observations were conducted at this colony (David et al. 1986). Interestingly, white sharks are not known to hunt Cape fur seals around the Kleinzsee and Van Reenan's Bay colonies, and so it appears that in the absence of predation risk these Cape fur seals show increased movement during warmer and brighter periods of the day. With very little daytime activity observed amongst Cape fur seal in Mossel Bay during this study, it appears unlikely that thermoregulatory needs play a role in traversing behaviour for this colony but rather that it might be scheduled around predation risk, as it seems to be in False Bay (Laroche et al. 2008).

White sharks are present and highly active in predating Cape fur seals in both Mossel Bay (Johnson et al. 2009a) and False Bay (Martin et al. 2005; Laroche et al. 2008; Martin et al. 2009). Based both on their ambush hunting behaviour (Martin et al. 2005; Martin & Hammerschlag 2012) and retinal morphology (Gruber 1975), white sharks most likely require at least some light to hunt. Correspondingly, predations in Mossel Bay and False Bay take place during all hours of the day but are more frequent and have the best success rates during crepuscular periods when Cape fur seals are less able to detect white sharks below them (Martin et al. 2005; Hammerschlag et al. 2006; Johnson et al. 2009a; Martin & Hammerschlag 2012). These diel shifts in predation risk were reflected by the reduced traversing frequency and increased group sizes of Cape fur seals observed during daytime and crepuscular periods in the present study.

Cape fur seal traversing patterns were also observed to change with season. In both False Bay and Mossel Bay, white sharks most actively hunt Cape fur seals between the months of May through September (Martin et al. 2005; Hammerschlag et al. 2006; Ryklief et al. 2014), corresponding to the period when Cape fur seal pups are just becoming mature enough to enter the water for the first time (David et al. 1986). The fewest traversing events overall were observed during winter in this study, and in particular, winter was the season when Cape fur seals were least likely to depart Seal Island during the day. Interestingly, Cape fur seals were observed to traverse in the highest frequencies during autumn and spring, suggesting the possibility of preparation and recovery phases around decreased foraging opportunities due to higher predation risk in winter. In addition, Cape fur seal group sizes were statistically the largest during autumn surveys (March to May). This pattern may correspond either to lactating females preferring to forage in groups, or possibly to heightened grouping behaviour during the newly-weaned pups' first month of entering the water (see De Vos et al. 2015). As the size and maturity of individuals were not recorded during surveys, this study is unable to infer which of the above scenarios might have been driving the larger group sizes in autumn months. Group sizes were smallest during summer months, indicating either that Cape fur seals might be less vigilant about finding safety in numbers during this season due to the decreased presence of white sharks around the colony (Ryklief et al. 2014), or possibly that individuals weaned the previous years were older and more experienced by the summer seasons.

The present study provides the first investigation into the effects of lunar cycle on Cape fur seal nocturnal traversing behaviour. Patterns closely aligned with observations that Galapagos fur seals avoid foraging at night during the full moon (Trillmich & Mohren 1981; Horning & Trillmich 1999). As mentioned previously, it can be difficult to tease apart whether this pattern is due to either predator avoidance or the effect of moon phase on the seals' feeding efficiency (Trillmich & Mohren 1981; Horning & Trillmich 1999). Horning and Trillmich (1999) proposed that the vertical migration of Galapagos fur seal prey during full moons might explain the reduced foraging behaviour they observed during these periods. A similar pattern could potentially occur with Cape fur seals (Kooyman & Gentry 1986; David 1987). Cape fur seal diet mostly comprises a variety of teleost fish species such as anchovy, pilchard and hake (David 1987; Punt et al. 1995), as well as a few cephalopod species (Lipinski & David 1990; de Bruyn et al. 2003). Hake species such as *Merluccius capensis* and *M. paradoxus* vertically migrate towards the surface at night in response to their prey (Pillar & Barange 1997) and full moon phases may potentially disrupt this migration. Furthermore, the vertical migration of certain squid species is affected by moon phase; *Dosidicus gigas* spends limited time in shallower waters on nights during full moon phases than during new moon phases (Gilly et al. 2006). Therefore it seems plausible that it may be less efficient for Cape fur seals to hunt during full moon periods.

Despite this, there was no reduction in the numbers of groups observed departing Seal Island during larger moon phases in the present study. However, the size of groups observed in the present study did increase significantly with moon size. The frequency of groups returning to the island at night-time did significantly decreased with moon size. However, this pattern also corresponded with significantly larger groups returning to Seal Island on these nights, suggesting that the lower frequencies of returning groups on moonlit nights was likely due to foraging Cape fur seals preferring to stay in larger groups during moonlit nights rather than return individually. These patterns suggest that the changes in Cape fur seal traversing behaviour with the lunar cycle might be more likely to do with predator-avoidance behaviour than foraging efficiency. Interestingly, Fallows et al. (2016) identified that the predation risk is reduced for Cape fur seals in False Bay over dawn periods during the full moon. These authors hypothesised that this may be due to the increased visual acuity of Cape fur seals from the added moonlight, enabling them to better detect and avoid white sharks lurking below. This hypothesis seems plausible, although moonlight did not significantly affect any aspect of Cape fur seal traversing behaviour during dawn hours in either False Bay (Fallows et al. 2016), or in Mossel Bay during the present study. Instead, nocturnal traversing behaviour observed in the present study supports the hypothesis that predation risk is likely to be higher for Cape fur seals during moonlit nights (Hammerschlag et al. 2006; Fallows et al. 2016).

While a comprehensive study on nocturnal predation activities of white sharks has not yet been published, night-time predations have been observed in Mossel Bay (R. Johnson unpublished data; Table 2). A moonlit sky may possibly provide ambient light conditions similar to that experienced during crepuscular periods where the sharks have a visual advantage over their prey and success rate of their attacks may be greater (Hammerschlag et al. 2006). Shoaling behaviour, or seeking 'safety in numbers' is a well-documented predator avoidance behaviour among marine prey species (Hager & Helfman 1991; Brown et al. 2001; White & Warner 2007; De Vos & O'Riain 2012), and in the case of Cape fur seals has also been observed to enable mobbing behaviour to fend off hunting white sharks (Johnson et al. 2009b). If Cape fur seals are at a greater risk of predation from white sharks during moonlit nights, then this predator avoidance strategy might explain the covariance of foraging group sizes and moonlight observed in this study.

Behavioural changes in response to increased predation risk during the full moon have been documented in many animals, particularly small mammals and birds (Lockard & Owings 1974; Clarke 1983; Gilbert & Boutin 1991; Kotler et al. 1991; Mougeot & Bretagnolle 2000). However, anthropogenic light from the town of Mossel Bay was not measured or controlled for within the present study, and could have also impacted nocturnal white shark predatory behaviour and/or Cape fur seal foraging behaviour. Analyses in the present study assumed that anthropogenic light might have impacted these predator-prey behaviours equally across night-time surveys, and therefore interpretation of these results should be made with this caveat in mind. Further studies investigating the effects of anthropogenic light on the predator-prey behaviour of white sharks and Cape fur seals in Mossel Bay are warranted, and could help to verify and further define the role of the moon in these interactions.

It is necessary to acknowledge that observations during this study were limited to only one section of Seal Island. It is possible that during certain periods or conditions that Cape fur seals were more likely to traverse to and/or from other parts of the island, and this could have influenced these results. Nonetheless, it was impossible during this study to monitor all sides of the island simultaneously (particularly at night), and so the section of Seal Island having the vast majority of Cape fur seal traffic was selected as the most meaningful location to make observations. It is therefore posited that patterns observed at this consistent location over the four years of data collection provide valuable information on the effects of environmental ambient light on relative patterns of Cape fur seal traversing behaviour. Overall, results presented here support existing literature that Cape fur seals adjust the timing and group size of their traversing events to minimise their risk of predation by white sharks (Hammerschlag et al. 2006; Laroche et al. 2008; Martin & Hammerschlag 2012). This study additionally provides evidence for the first time that Cape fur seals increase the size of their groups while foraging in brighter moonlight conditions, and it is hypothesised that this helps them to minimise their risk of nocturnal predations by the ocean's apex predator. Future investigations on the influence of the lunar cycle on white shark nocturnal hunting behaviour will help to further define the dynamic interplay between predator and prey in South Africa's waters.

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TABLES:

Table 1. The details of 69 field surveys observing Cape fur seal (*Arctocephalus pusillus pusillus*) traversing behavior at Seal Island in Mossel Bay, South Africa are outlined below. 'MFI' stands for 'moon face illuminated' given as a proportion, and all cases of 'observation' are abbreviated to 'Obs.' The daytime observation point is provided in the fifth column, however all dawn, dusk and night observations were recorded from the research boat.

Survey	Start Date	Season	MFI	Daytime Obs. Point	Dawn Obs. Time	Day Obs. Time	Dusk Obs. Time	Night Obs. Time	Total Obs. Time	Traversing Events
1	16/07/2008	Winter	0.98	Hotel	2 h 0 m	8 h 7 m	2 h 0 m	11 h 53 m	24 h 0 m	131
2	08/08/2008	Winter	0.52	Hotel	2 h 0 m	8 h 39 m	2 h 0 m	11 h 21 m	24 h 0 m	225
3	14/08/2008	Winter	0.96	Hotel	2 h 0 m	8 h 50 m	2 h 0 m	11 h 10 m	24 h 0 m	200
4	11/09/2008	Spring	0.88	Hotel	-	-	0 h 20 m	1 h 40 m	2 h 0 m	28
5	15/09/2008	Spring	0.99	Hotel	2 h 0 m	9 h 52 m	2 h 0 m	10 h 8 m	24 h 0 m	195
6	22/09/2008	Spring	0.41	Hotel	2 h 0 m	10 h 8 m	2 h 0 m	9 h 52 m	24 h 0 m	315
7	25/09/2008	Spring	0.12	Hotel	2 h 0 m	10 h 15 m	1 h 0 m	9 h 45 m	23 h 0 m	280
8	30/10/2008	Spring	0.04	Hotel	2 h 0 m	11 h 26 m	2 h 0 m	8 h 34 m	24 h 0 m	298
9	10/11/2008	Spring	0.93	Hotel	2 h 0 m	11 h 38 m	0 h 38 m	8 h 14 m	22 h 30 m	284
10	21/11/2008	Spring	0.29	Hotel	2 h 0 m	12 h 3 m	2 h 0 m	7 h 57 m	24 h 0 m	226
11	27/11/2008	Spring	0.03	Hotel	2 h 0 m	12 h 10 m	2 h 0 m	7 h 50 m	24 h 0 m	21
12	27/11/2008	Spring	0.03	Hotel	0 h 46 m	-	0 h 24 m	7 h 50 m	9 h 0 m	231
13	08/02/2009	Summer	0.99	Hotel	2 h 0 m	11 h 32 m	2 h 0 m	8 h 28 m	24 h 0 m	141
14	02/03/2009	Autumn	0.35	Hotel	2 h 0 m	9 h 39 m	1 h 8 m	9 h 13 m	22 h 0 m	234
15	10/03/2009	Autumn	1.00	Hotel	2 h 0 m	10 h 30 m	2 h 0 m	9 h 30 m	24 h 0 m	97
16	24/03/2009	Autumn	0.03	Hotel	2 h 0 m	10 h 0 m	2 h 0 m	10 h 0 m	24 h 0 m	273
17	22/04/2009	Autumn	0.06	Hotel	1 h 0 m	9 h 1 m	2 h 0 m	10 h 59 m	23 h 0 m	221
18	12/05/2009	Autumn	0.87	Hotel	2 h 0 m	8 h 25 m	2 h 0 m	11 h 35 m	24 h 0 m	354
19	11/06/2009	Winter	0.85	Hotel	2 h 0 m	7 h 54 m	2 h 0 m	12 h 6 m	24 h 0 m	323
20	02/07/2009	Winter	0.83	Hotel	2 h 0 m	7 h 55 m	2 h 0 m	12 h 5 m	24 h 0 m	139
21	09/07/2009	Winter	0.94	Hotel	2 h 0 m	7 h 59 m	2 h 0 m	12 h 1 m	24 h 0 m	121
22	06/08/2009	Winter	0.99	Hotel	2 h 0 m	8 h 36 m	2 h 0 m	11 h 24 m	24 h 0 m	150
23	20/08/2009	Winter	0.01	Hotel	2 h 0 m	9 h 1 m	2 h 0 m	10 h 59 m	24 h 0 m	203
24	09/09/2009	Spring	0.72	Hotel	2 h 0 m	9 h 40 m	2 h 0 m	10 h 20 m	24 h 0 m	130
25	25/09/2009	Spring	0.48	Hotel	2 h 0 m	10 h 14 m	2 h 0 m	9 h 46 m	24 h 0 m	181
26	08/10/2009	Spring	0.76	Hotel	2 h 0 m	10 h 41 m	2 h 0 m	9 h 19 m	24 h 0 m	278
27	05/11/2009	Spring	0.87	Hotel	2 h 0 m	11 h 37 m	2 h 0 m	8 h 23 m	24 h 0 m	235
28	22/11/2009	Spring	0.16	Hotel	2 h 0 m	12 h 5 m	2 h 0 m	7 h 55 m	24 h 0 m	163
29	17/02/2010	Summer	0.13	Hotel	2 h 0 m	11 h 14 m	2 h 0 m	8 h 46 m	24 h 0 m	232
30	05/03/2010	Autumn	0.67	Hotel	2 h 0 m	10 h 41 m	2 h 0 m	9 h 19 m	24 h 0 m	224
31	02/04/2010	Autumn	0.82	Hotel	2 h 0 m	9 h 41 m	2 h 0 m	10 h 19 m	24 h 0 m	288
32	14/04/2010	Autumn	0.00	Hotel	2 h 0 m	9 h 17 m	2 h 0 m	10 h 43 m	24 h 0 m	430
33	20/04/2010	Autumn	0.42	Hotel	2 h 0 m	9 h 4 m	2 h 0 m	10 h 56 m	24 h 0 m	260
34	17/05/2010	Autumn	0.18	Hotel	2 h 0 m	8 h 19 m	2 h 0 m	11 h 41 m	24 h 0 m	290
35	26/05/2010	Autumn	0.99	Hotel	2 h 0 m	8 h 7 m	2 h 0 m	11 h 53 m	24 h 0 m	337
36	16/06/2010	Winter	0.26	Hotel	2 h 0 m	7 h 53 m	2 h 0 m	12 h 7 m	24 h 0 m	210
37	12/07/2010	Winter	0.02	Hotel	2 h 0 m	8 h 2 m	2 h 0 m	11 h 58 m	24 h 0 m	73
38	05/08/2010	Winter	0.22	Hotel	2 h 0 m	8 h 34 m	2 h 0 m	11 h 26 m	24 h 0 m	132
39	12/08/2010	Winter	0.12	Hotel	2 h 0 m	8 h 46 m	2 h 0 m	11 h 14 m	24 h 0 m	147
40	06/09/2010	Spring	0.03	Hotel	2 h 0 m	9 h 33 m	2 h 0 m	10 h 27 m	24 h 0 m	321
41	13/09/2010	Spring	0.37	Hotel	2 h 0 m	9 h 48 m	2 h 0 m	10 h 12 m	24 h 0 m	198
42	22/09/2010	Spring	1.00	Hotel	2 h 0 m	10 h 7 m	2 h 0 m	9 h 53 m	24 h 0 m	166
43	27/09/2010	Spring	0.81	Hotel	2 h 0 m	10 h 18 m	2 h 0 m	9 h 42 m	24 h 0 m	88
44	20/10/2010	Spring	0.96	Hotel	2 h 0 m	11 h 6 m	2 h 0 m	8 h 54 m	24 h 0 m	337
45	04/11/2010	Spring	0.02	Hotel	2 h 0 m	11 h 35 m	2 h 0 m	8 h 25 m	24 h 0 m	342
46	28/11/2010	Spring	0.49	Hotel	2 h 0 m	12 h 12 m	2 h 0 m	7 h 48 m	24 h 0 m	262
47	22/02/2011	Summer	0.71	Boat	-	-	1 h 7 m	4 h 53 m	6 h 0 m	60
48	15/03/2011	Autumn	0.00	Boat	-	4 h 43 m	1 h 17 m	-	6 h 0 m	7
49	21/03/2011	Autumn	0.00	Boat	-	4 h 45 m	1 h 15 m	-	6 h 0 m	24
50	30/03/2011	Autumn	0.35	Boat	1 h 27 m	-	-	4 h 33 m	6 h 0 m	190
51	05/04/2011	Autumn	0.00	Boat	0 h 44 m	5 h 16 m	-	-	6 h 0 m	19
52	12/04/2011	Autumn	0.56	Boat	1 h 8 m	-	-	4 h 52 m	6 h 0 m	167
53	25/04/2011	Autumn	0.71	Boat	-	0 h 28 m	2 h 0 m	3 h 32 m	6 h 0 m	55
54	28/04/2011	Autumn	0.16	Boat	-	0 h 54 m	2 h 0 m	3 h 6 m	6 h 0 m	102
55	04/05/2011	Autumn	0.01	Boat	2 h 0 m	1 h 51 m	-	2 h 2 m	5 h 53 m	84
56	10/05/2011	Autumn	0.00	Boat	-	5 h 58 m	-	-	5 h 58 m	20
57	27/05/2011	Autumn	0.30	Boat	2 h 0 m	1 h 6 m	-	2 h 12 m	5 h 18 m	50
58	04/06/2011	Winter	0.05	Boat	2 h 0 m	1 h 30 m	-	2 h 30 m	6 h 0 m	117
59	06/06/2011	Winter	0.27	Boat	-	-	-	6 h 0 m	6 h 0 m	133
60	06/10/2011	Winter	0.61	Boat	2 h 0 m	1 h 40 m	-	2 h 20 m	6 h 0 m	73
61	14/06/2011	Winter	0.99	Boat	-	0 h 24 m	2 h 0 m	10 h 52 m	13 h 16 m	217
62	17/06/2011	Winter	0.94	Boat	2 h 0 m	2 h 0 m	2 h 0 m	12 h 7 m	18 h 7 m	127
63	22/06/2011	Winter	0.55	Boat	2 h 0 m	1 h 53 m	2 h 0 m	12 h 7 m	18 h 0 m	196
64	23/06/2011	Winter	0.45	Boat	-	-	-	6 h 0 m	6 h 0 m	47
65	29/06/2011	Winter	0.44	Boat	-	-	0 h 2 m	3 h 28 m	3 h 30 m	23
66	07/06/2011	Winter	0.36	Boat	2 h 0 m	1 h 57 m	2 h 0 m	12 h 3 m	18 h 0 m	160
67	14/07/2011	Winter	1.00	Boat	2 h 0 m	2 h 4 m	2 h 0 m	11 h 56 m	18 h 0 m	187
68	09/12/2011	Summer	0.18	Boat	-	-	1 h 34 m	4 h 26 m	6 h 0 m	30
69	18/12/2011	Summer	0.00	Boat	-	6 h 0 m	-	-	6 h 0 m	42
Totals					**107 h 5 m**	**474 h 43 m**	**104 h 45 m**	**564 h 59 m**	**1,251 h 32 m**	**12,144**

Table 2. The times and metadata are provided for the four white shark (*C. carcharias*) predations on Cape fur seals (*Arctocephalus pusillis pusillus*) that were observed during 69 surveys at Seal Island in Mossel Bay, South Africa from 2008 to 2011.

Survey	Date	Time	Period	Season	MFI
3	14/08/2008	18:23	Dusk	Winter	0.96
8	30/10/2008	08:44	Day	Spring	0.04
16	24/03/2009	02:52	Night	Autumn	0.03
18	12/05/2009	01:16	Night	Autumn	0.87

FIGURES:

Figure 1. Traversing behaviour of Cape fur seals departing and entering the colony at Seal Island was observed from two locations shown below. Observations were focused on the radial section of Seal Island labelled 'Sector 2' where the majority of traversing events occurred.

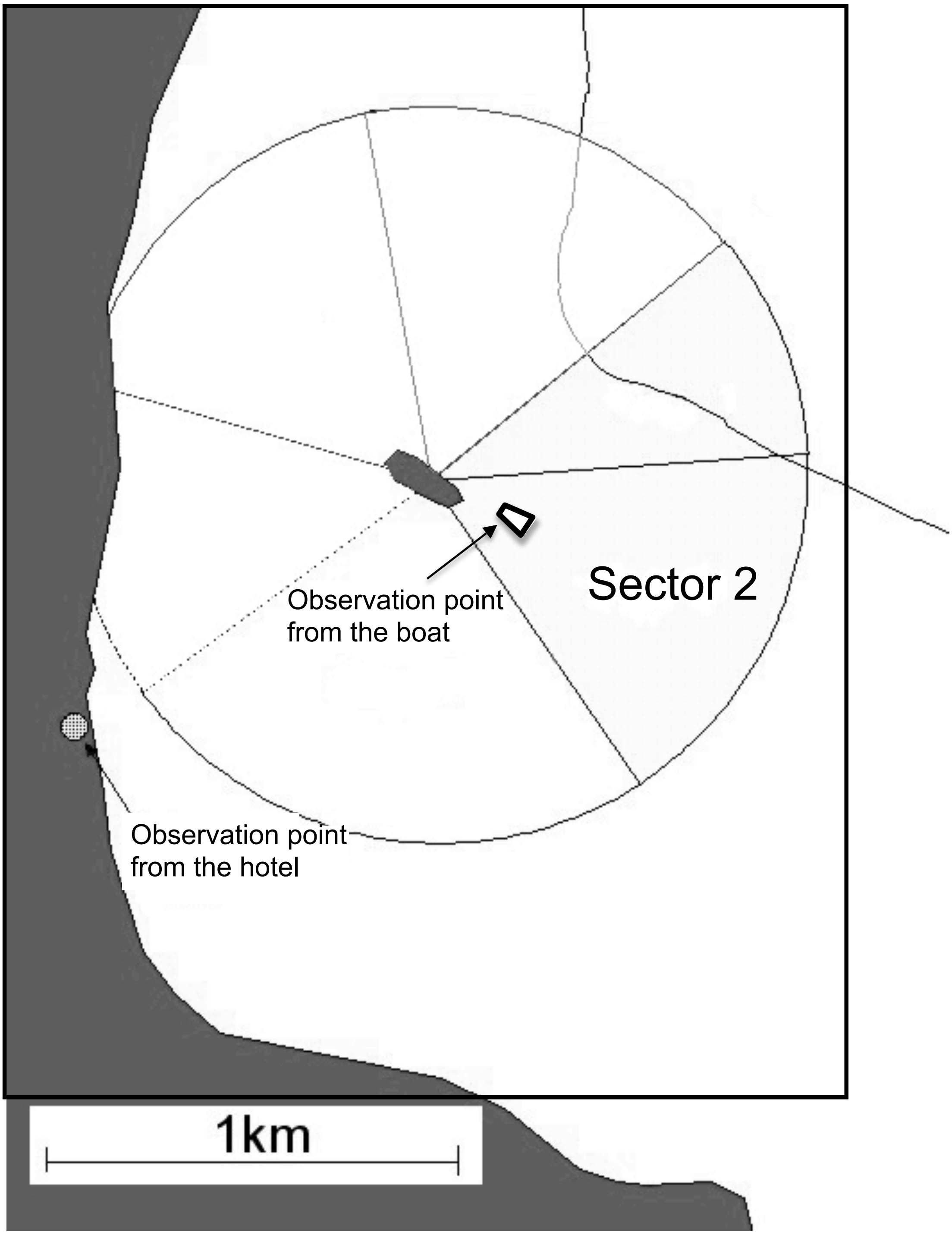

Figure 2. The rates of Cape fur seal groups traversing to and from Seal Island per hour over 69 surveys from July 2008 to December 2011 are represented below. Boxplots illustrate median frequencies of groups per hour, with 25th and 75th percentiles and ranges.

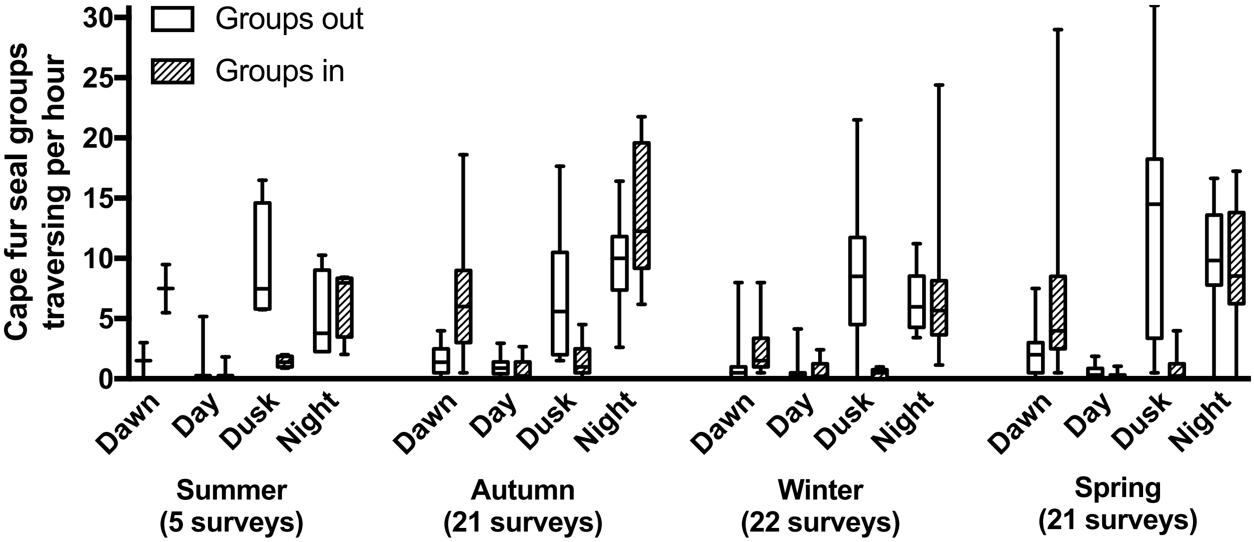

Figure 3. The rates of different size classes of Cape fur seal groups departing and returning to Seal Island at each diel period are illustrated below. The bars and whiskers represent mean groups per hour and standard error respectively.

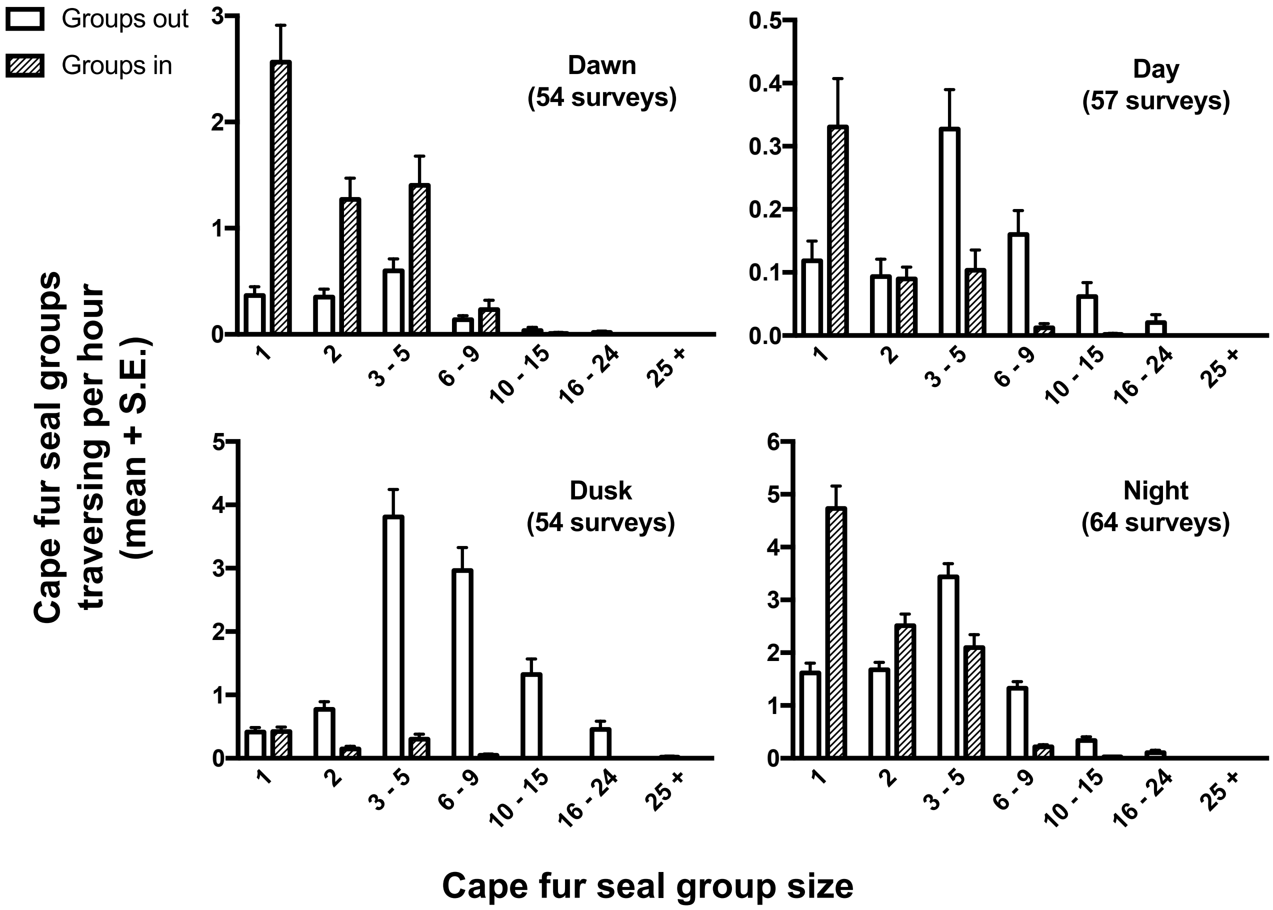

Figure 4. The relative frequencies of different size classes of Cape fur seal groups departing and returning to Seal Island per hour during each season are illustrated below. The bar portions and whiskers represent mean groups per hour and standard error respectively.

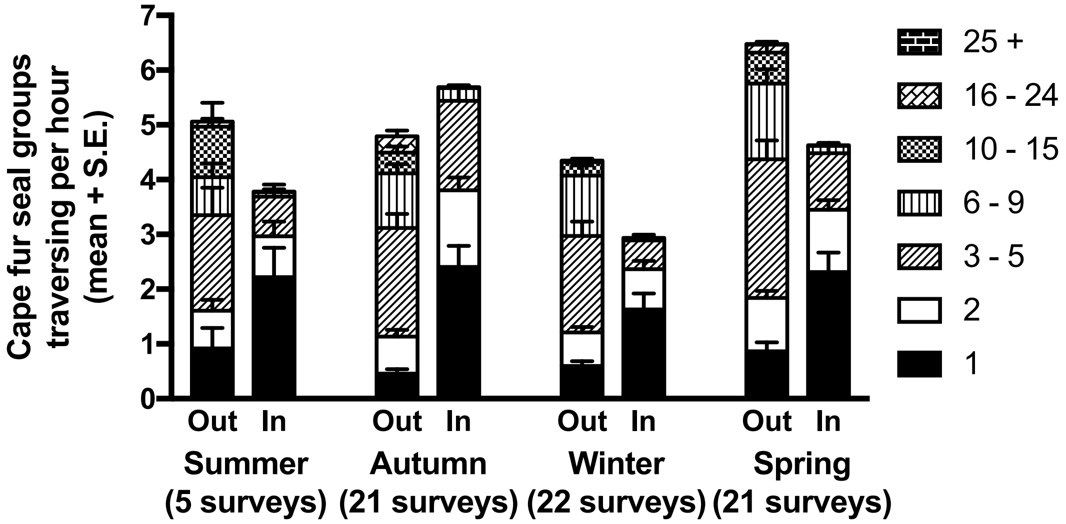

Figure 5. The relationship between the proportion of moon face illuminated (MFI) and the mean frequency of Cape fur seal groups returning to Seal Island per hour of night-time surveys is illustrated below. The solid line represents the mixed-effects Poisson regression equation: $y = e^{(-0.289x + 2.354)}$; $P < 0.001$.

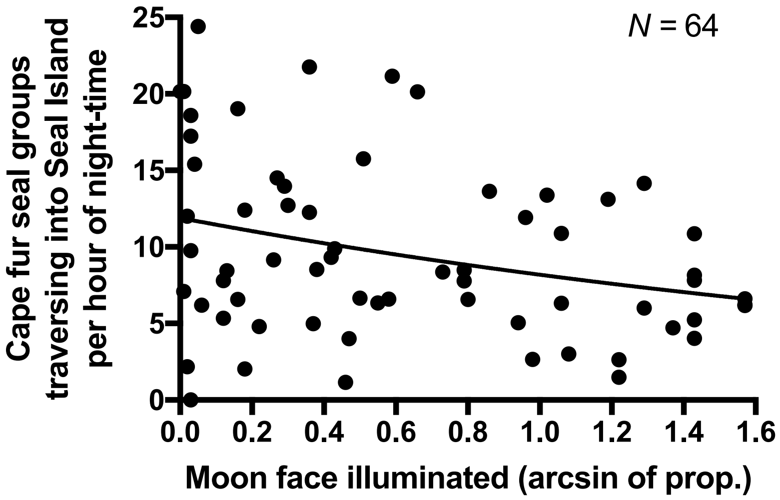

Figure 6. The probability of observing larger Cape fur seal group sizes among the 64 night-time surveys increased significantly with the proportion of moon face illuminated (MFI) for both departing (P < 0.001) and returning groups (P = 0.035). Boxplots illustrate median MFI at the time of observation, with the 25th and 75th percentiles and ranges. Mean MFI for each size class are represented with '+'. The median line for departing group size class '16 – 24' is overlapping with the 75th percentile of this group.