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WILDLIFE RESEARCH

Absence or avoidance? White shark response to killer whale predation risk

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ABSTRACT

Context. White sharks (*Carcharodon carcharias*) globally display seasonal site fidelity to coastal aggregations across their range, yet the prolonged absences from these aggregations have often been linked to the presence and predation by killer whales (*Orcinus orca*). This was the case following a predation event in 2015 at the Neptune Islands, when white sharks became abnormally absent for more than 2 months. However, how much this prolonged absence at the Neptune Islands was influenced by the predation event is unknown. **Aims.** Our study assessed whether the 69-day white shark absence in early 2015 was due to a predation event by killer whale in February 2015, or if such extended absence can reflect natural variations in residency at aggregations. **Methods.** We analysed 12 years (2013–2024) of white shark sighting records from wildlife tourism operators and acoustic telemetry data to investigate patterns of shark presence before and after the 2015 killer whale predation event, a shark mortality, and a killer whale sighting. **Key results.** White sharks exhibited six prolonged absences (mean absence duration + 3 standard deviations) across the 12-year study period, with the longest absence being 92 days, which was longer than the absence recorded in 2015 following killer whale predation (69 days). The number and extent of prolonged absences suggest that these departures are not unique to the 2015 event and may instead reflect natural or random variation in residency. **Conclusions.** Our findings showed that although killer whale predation and presence can trigger immediate responses and departure from aggregation sites, they are unlikely to be the sole driver of prolonged white shark absences at the Neptune Islands. **Implications.** Prolonged absences of white sharks may be influenced by killer whale predation as well as other predator–prey interactions and environmental factors. Integrative, long-term monitoring of all prey and predators is critical for understanding site fidelity and absence behaviour of white sharks.

Keywords: acoustic telemetry, cetaceans, displacement, elasmobranchs, fearscape, predator–prey, risk avoidance, top predator.

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Introduction

From the pack-ice to the equator, killer whales (*Orcinus orca*) are globally distributed predators (Forney and Wade 2006). With a high dietary diversity and capacity to develop complex foraging specialisations, they play a key role as top predators, shaping ecosystems through top-down predation and by creating a landscape of fear (Estes *et al.* 1998; Lefort *et al.* 2020; Matthews *et al.* 2020; Towner *et al.* 2022). Among their wide range of prey, killer whales have been observed preying on other top predators, including large sharks (Pyle *et al.* 1999; Ford *et al.* 2011; Ayres *et al.* 2024). Such interactions, once considered rare, have now been documented across multiple ocean basins (e.g. Visser 2005; Mucientes and Gonzalez-Pestana 2020; Terrapon *et al.* 2024), suggesting that sharks may be a more common prey item for killer whales than was previously assumed. Although interactions between killer whales and white sharks (*Carcharodon carcharias*) have not often been directly observed, such interactions have recently garnered global attention, with evidence of direct predation by killer whales on white sharks having been increasingly

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documented off South Africa, California, and Australia (Jorgensen *et al.* 2019; Towner *et al.* 2022; Reeves *et al.* 2025).

These predation events have shaped the theory that killer whale predations can cause abrupt displacement and prolonged absences of top predatory sharks, including white sharks. This has been supported by observations in South Africa, Mexico and the Farallon Islands, where predation by killer whales has been linked to abrupt displacement of several shark species for periods of several weeks to months or complete absence from the site, including white sharks, and can lead to subsequent ecosystem cascades (Jorgensen *et al.* 2019; Towner *et al.* 2022; Bowlby *et al.* 2023; Engelbrecht 2023; Towner *et al.* 2023; Ayres *et al.* 2024). However, all locations have not been affected by killer whale predation in a similar way. Repeated annual predations and frequent predations by killer whale in South Africa have led to long-term site abandonment (Towner *et al.* 2022), whereas predations at the Farallon Islands are infrequent and isolated, and have resulted in absences ranging approximately one week to 8 months (Jorgensen *et al.* 2019). In addition to predation risk, necromones from decomposing shark tissue may trigger departure responses and contribute to white shark avoidance of sites where killer whales have predated on other sharks (Stroud *et al.* 2014). These examples support that killer whales can displace white sharks from key aggregation sites, either through direct predation or indirectly via the fear of potential predation (Brown *et al.* 1999; Laundré *et al.* 2010), for prolonged periods. However, presence and residency at aggregation sites are also affected by various factors such as prey availability or thermal cues (Martin *et al.* 2009; Spurgeon *et al.* 2022), and absences typically occur when more abundant food is available elsewhere (Brown *et al.* 2010) or when environmental conditions become less suitable (Lee *et al.* 2021). Although killer whales can influence local shark behaviour and lead to prolonged absences (Jorgensen *et al.* 2019; Towner *et al.* 2022), the mechanisms driving white shark displacement, whether through direct predation, fear of predation, or avoidance of areas near white shark carcasses, and the extent of killer whale–driven absences, remain unclear.

Sharks are natural preys for Australian killer whales with documented predation (but no known resulting shark absences) on species such as blue sharks (*Prionace glauca*), shortfin makos (*Isurus oxyrinchus*), and tiger sharks (*Galeocerdo cuvier*), sometimes involving liver removal (Morrice 2004; Totterdell 2016; Reeves *et al.* 2025). Notably, at least three interactions with white sharks have been reported in southern Australia, including the following: (1) a presumed kill at the Neptune Islands Group Marine Park (henceforth referred to as the 'Neptunes Islands') in 2015 (Matt Waller, pers. comm.; youtube.com/watch?v=WC8Wxfn5xFw), which garnered substantial public attention and after which white sharks were not sighted for ~2 months, leading the public to compare this event to the disappearance of white sharks in South Africa, (2) an encounter near Kangaroo Island in 2021, where two killer whales attacked a white shark, although it is unclear whether the shark survived, and (3) a kill in Portland (south-eastern Australia) in 2023, confirmed on the basis of DNA evidence and citizen science observations (Reeves *et al.* 2025).

Our study used 12-year sighting and acoustic telemetry datasets to investigate whether the prolonged white shark absence from the Neptune Islands after the 2015 predation event were driven by the killer whale interaction or part of natural variation in the abundance and residency of white sharks. If prolonged white shark absences also occur when killer whales are absent, it would suggest that other drivers beyond fear-based avoidance might have contributed to the 2-month disappearance of white sharks. Our findings contribute to a broader understanding of predator–prey dynamics between top marine predators.

Materials and methods

Study site

The Neptune Islands (35°14′20″S, 136°4′10.92″E), located ~70 km south of Port Lincoln, South Australia, is the only location in Australia where white shark commercial cage-diving is permitted. White sharks at the Neptune Islands are transient or temporary resident and only remain around the islands from a few days to weeks, rarely staying longer than a month. Although white sharks can be sighted at the Neptune Islands all year around, sex-biased seasonal peaks occur with the number of males increasing in late spring and summer, and females being more abundant in autumn (Bruce and Bradford 2015; Nazimi *et al.* 2018). Most white sharks are subadults to adults, ranging from 3.5 to 4.5 m in total length, but small juveniles (~2 m total length) and large adults (>5 m total length) are also sporadically sighted. These islands host one of Australia's largest breeding colony of long-nosed fur seals (*Arctocephalus forsteri*), which attract white sharks to the area (Shaughnessy 2006; Bruce and Bradford 2012), as well as various pelagic and benthic fishes such as silver trevally (*Pseudocaranx* sp.), southern eagle rays (*Myliobatis australis*), Australian salmon (*Arripis trutta*), southern bluefin tuna (*Thunnus maccoyii*), yellowtail kingfish (*Seriola lalandi*), and horseshoe leatherjacket (*Meuschenia hippocrepis*) (Meyer *et al.* 2020; Dennis *et al.* 2024; Whitmarsh *et al.* 2025).

Shark sightings data

As part of the white shark cage-diving license policy and monitoring program established in 2013 (Niella *et al.* 2023), cage-diving operators are required to record daily activity and number of individual sharks sighted. Individual white sharks were identified using established white shark identification methods (Domeier and Nasby-Lucas 2007; Anderson *et al.* 2011), where a combination of pigmentation patterns (countershading, rosettes, islets, freckles, spots), notches or scoops, amputations,

scoliosis, and scarring are used to identify individuals on the basis of their unique variation in these physical characteristics.

Observation description

On 2 February 2015, crew and tourists onboard one of cage-diving vessels (Shark Warrior, operated by Adventure Bay Charters) noticed a group of approximately six killer whales moving towards their boat anchored on the north-eastern tip of North Neptune Islands (35°19′12″S, 136°07′12″E). Witnesses documented that the killer whales (sometimes within 20 m of the vessel) began to attack a white shark approximately 20 m off the stern of the vessel. Three of the killer whales seemed to engage in corralling behaviour around the shark, restricting its movement and ability to escape harassment from the killer whales. Throughout this period the killer whales occasionally used their rostra to ram the shark's flank.

At one point, a larger, presumably adult, male killer whale, sexed on the basis of the diagnostic shape of the large erected dorsal fin, could briefly be seen at the surface holding the shark in its mouth before the shark broke away at speed. The killer whales continued to attack the flank of the shark until eventually a killer whale breached and landed on the shark. At this time, all individuals from the group submerged. Shortly after the pod submerged, an oil slick appeared on the surface, and the shark was not sighted again. This event lasted for ~1 h. Following this event and based on the daily white shark cage-diving sighting log, no white shark was sighted until 11 April 2015 (69 days after the event).

This description is based on the YouTube video (youtube.com/watch?v=WC8Wxfn5xFw) and eye-witness account (Matt Waller, pers. comm.) as the original video recording could not be found.

Shark tagging

Since September 2013, we deployed and maintained two acoustic receivers (VR2W and VR2AR; Innovasea, Nova Scotia, Canada) at North Neptune Islands and one at South Neptune Islands. From August 2018, an additional 13 receivers were deployed around North Neptune Islands for fine-scale movement studies, with ~80% detection probability at ~300 m. Six were placed on the northern side (219–284 m spacing), six on the southern side (228–283 m), and one at a central transition zone (Niella *et al.* 2023, 2024). In 2024, the array was reduced, and only the two receivers at North Neptune Islands remained as part of the long-term monitoring effort. Receivers were last downloaded for this study in August 2024. White sharks were tagged with acoustic transmitters (Innovasea V16–6H; 70–150 s random interval, battery life 10 years) attached to umbrella dart heads via 100–150 mm stainless steel wire (1.6 mm diameter) and implanted into the dorsal musculature using a modified spear gun (Meyer *et al.* 2018; Niella *et al.* 2023). From 2013–2024, there were 207 white sharks tagged, with 17 ± 1.75 (mean ± s.e.) individuals tagged per year. This research was conducted under the Department for Environment and Water permit number Q26292 and tagging was undertaken under Flinders University ethics approval number E398 and E464-17.

Data analysis

We used the daily shark sighting data from November 2013 to 2024 to estimate mean weekly sightings accounting for days when operators were not present at the Neptune Islands, by dividing total weekly sightings by the number of days operators were present that week. We addressed gaps in survey effort for the sighting data by imputing short no-boat periods on the basis of surrounding presence/absence data. Single no-boat days were imputed to match the preceding and following day if they were the same; if they differed, the day was imputed as presence, assuming presence takes precedence. For two consecutive no-boat days, both were imputed only if the bounding days matched; if not, they were left as missing and excluded from analysis. As a result, absence durations may be somewhat conservative and are likely to represent an underestimate of true absences. Time series of presence and absences between 2013 and 2024 were also shown by plotting the number of sharks sighted and number of sharks detected across month.

Our study focused on prolonged absences, which were defined by mean absence + 3 standard deviations (mean absence was: 7.9 days ± 11.2 s.d.); these absences were too rare to use statistical analysis and identify drivers of occurrences. Factors such as seal abundance or presence of southern bluefin tuna, and a nearby tuna aquaculture industry might have also affected the visitation pattern and absences of white sharks at the Neptune Islands. However, seal abundance at the Neptune Islands, the tuna migration, and the operation of the tuna aquaculture industry are seasonal and would therefore expect to affect white shark presence seasonally rather than drive the rare, prolonged absences we are investigating here. In addition, many factors that would be worth including in a quantitative analysis do not have the data available to do so. For example, seal abundance should be included, but a fur seal census of the Neptune Islands has not been undertaken since 2013–14 (Shaughnessy *et al.* 2015). We conducted all analyses in RStudio (ver. 2022.07.1, Team 2016).

Results and discusssion

Our study used acoustic telemetry and sighting datasets to examine whether prolonged white shark absences from the Neptune Islands following the 2015 predation event were driven by interactions with killer whales, or whether similar absences occur in the absence of killer whales, indicating that other drivers beyond fear-based avoidance might have contributed to the 69-day disappearance of white sharks.

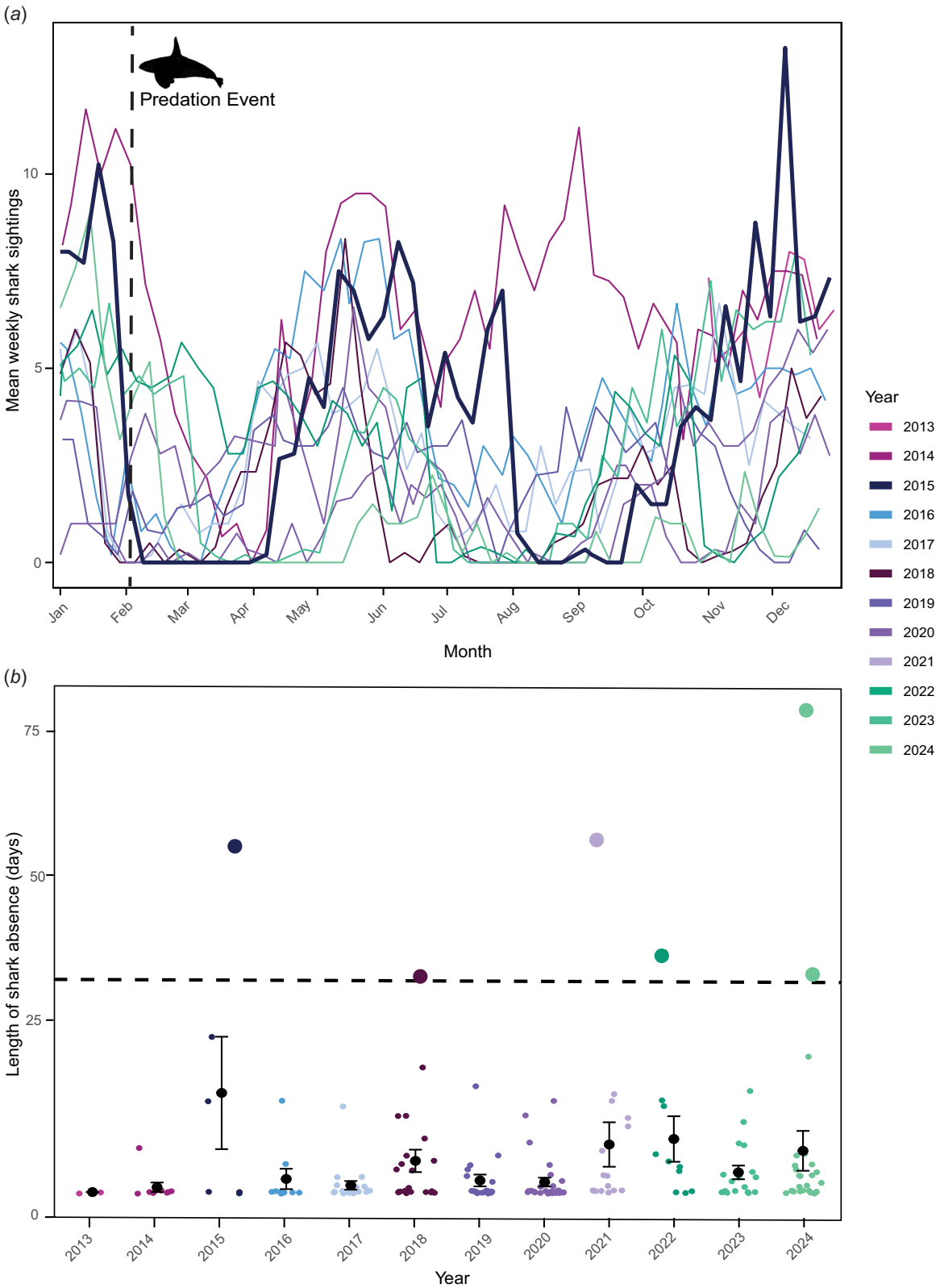

Fig. 1. (*a*) Mean weekly white shark (*Carcharodon carcharias*) sightings per month from 2013 to 2024 at the Neptune Islands Group Marine Park (South Australia). The killer whale (*Orcinus orca*) icon and vertical dashed line indicate a killer whale predation event on a white shark on 2 February 2015. (*b*) Duration of absences across the study period. Horizontal dashed line represents ± 3 s.d. above the mean, with the circles with error bars representing mean and standard deviation.

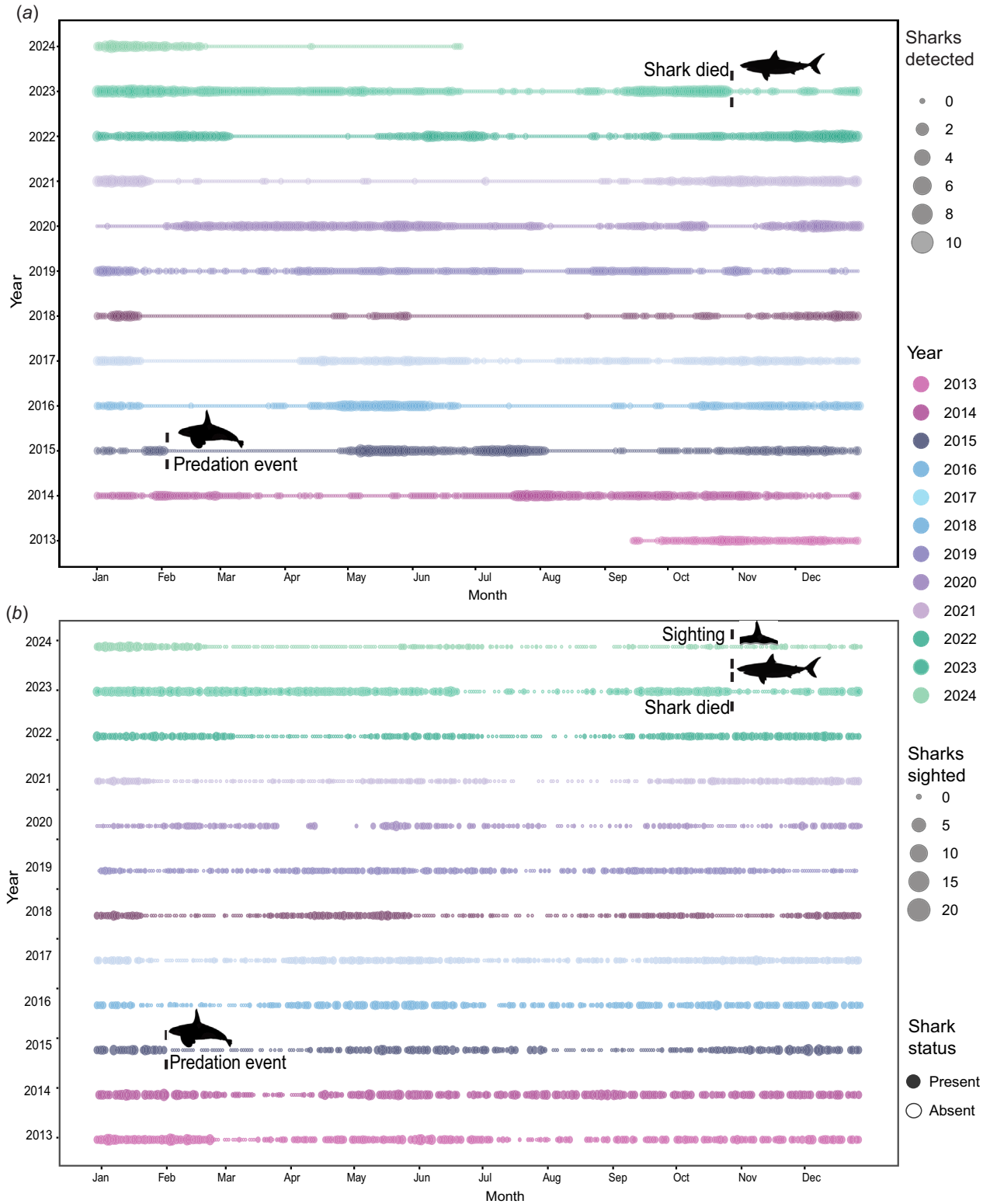

Fig. 2. Daily occurrence of white sharks (*Carcharodon carcharias*) at Neptune Island Group Marine Park (2013–2024) on the basis of (*a*) number of acoustically tagged sharks detected per day and (*b*) number of sharks sighted by cage-diving operators per day, with days with no effort represented as gaps within the timeline. The killer whale (*Orcinus orca*) icon represent a killer whale predation event on a white shark on 2 February 2015. The shark icon indicates a deceased individual, and the killer whale fin indicates a confirmed sighting. The vertical dashed line indicates start of the event.

The ongoing Neptune Islands white shark cage-diving industry monitoring program established since 2013 offered a unique opportunity to examine the frequency and duration of prolonged white shark absences from an otherwise consistent aggregation. This opportunity enabled us to contextualise the effects of predations by killer whales on white shark presence and site fidelity.

The number of sharks detected and sighted typically peaks at the Neptune Islands from November to January and again from late April to June, with a trough in abundance in February–March and July–August (Figs 1*a*, 2; Bruce and Bradford 2015; Nazimi *et al.* 2018). However, this pattern is highly variable and has been particularly unpredictable since 2021, with 2024 being the least consistent year in terms of sightings, detections, and residency (Figs 1, 2). Following the predation event in 2015, sharks were absent for 69 days in most of February–March 2015. This is consistent with reports that killer whale presence can trigger abrupt white shark departures (Jorgensen *et al.* 2019; Towner *et al.* 2022). The sudden departure of white sharks from the Neptune Islands mirrors that of the Farallon Islands (Jorgensen *et al.* 2019), and early responses to killer whale predation in South Africa (Towner *et al.* 2022). As a result, it was proposed that the prolonged white shark absence at the Neptune Islands was due to the killer whale predation. White sharks from South Africa and Australia are also part of the same highly connected genetic stock (Laso-Jadart *et al.* 2025) and could, therefore, be assumed to have similar responses to predation risk. However, the killer whale predation on a white shark at the Neptune Islands occurred during a period when white shark presence and abundance at the Neptune Islands are often low, with white sharks being also absent for most of February–March in 2016, 2017, 2018, and 2024 (Table 1, Figs 1, 2). While this could be a learnt response to avoid the area at this time of the year because of the 2015 events, low presence or abundance during these months were also observed before 2015 (A. Fox and A. Wright, pers. comm.). This prolonged absence was also not a unique event because we observed five other prolonged absences over the 12-year study period, lasting from 42 days in 2018 to 92 days in 2024 (Fig. 1*b*). Given the timing of the absence in 2015 and other prolonged absences, it is unclear whether the predation event directly caused the prolonged disappearance of white sharks. The timing of the 2015 prolonged absence did not coincide with other activities suggested to influence white shark presence at the Neptune Islands. For example, the annual towing and harvesting of southern bluefin tuna off Boston Bay, 60 km north of North Neptune Islands, which could attract white sharks away from the Neptune Islands mostly occurs in January and in May–July respectively. Neither of which could therefore explain the sudden exodus and prolonged white shark absence in February 2015. The cause of these prolonged absences is currently unknown and might be driven by the availability of food (e.g. whale carcasses) in other areas attracting white sharks away from the Neptune Islands for extended periods. Although seasonal absences occur at other white shark aggregations as part of regular seasonal movement patterns, for example, Seal Island (False Bay; Kock *et al.* 2013), Cape Cod (Massachusetts; Curtis *et al.* 2014), white sharks can occur at the Neptune Islands throughout the year and the prolonged absences observed here are not part of seasonal availability of food (e.g. related to fur seal breeding cycle or tuna migrations). Capturing and deploying fin-mounted satellite tags or internal acoustic tags can also result in white shark leaving the tagging location (Butcher *et al.* 2023). However, these tags or deployment methods were not used at the Neptune Islands or surrounding area during the study period and therefore cannot explain the departure and prolonged absence. The deployment of external tags is also unlikely to have affected the residency or presence of white sharks (Niella *et al.* 2023), especially because no tagging had occurred within a week of the observed white shark departure.

It is possible that killer whales were present and not sighted during the other prolonged absences, but cage-diving operators are at the Neptune Islands for 10–12 days per fortnight, reducing the likelihood of killer whale sightings being missed. In addition, a well-established citizen science program has recorded only an average of one killer whale sighting per year in this area or nearby regions (Killer Whales Australia, unpubl. data). Although citizen science programs are opportunistic and can be biased by effort, it is likely that the presence of killer whale in proximity to the Neptune Islands would have been detected and reported by one of the many recreational or

Table 1. Longest white shark absences (*Carcharodon carcharias*) in February–March on the basis of sightings and acoustic telemetry detections at the Neptune Islands, South Australia, from 2014 to 2024; note that 2013 was excluded because data were unavailable for those months.

Year	Sighting data		Detection data	
	Longest white shark absences (days)	Number of days with at least one shark sighted	Longest white shark absences (days)	Number of days with at least one shark detected
2014	5	38	7	49
2015[A]	58	1	56	3
2016	18	20	36	9
2017	15	21	59	0
2018	16	14	59	0
2019	6	31	7	21
2020	4	38	2	57
2021	18	6	29	8
2022	15	28	25	34
2023	2	44	0	59
2024	38	17	38	21

[A]2015 was the year of the killer whale predation at the islands.

Table 2. Mean number of white shark (*Carcharodon carcharias*) sightings and detected through acoustic telemetry a week before, during, and after key events at the Neptune Islands, South Australia.

Event type	Date	Days absent	Sighting data		Detection data	
			Mean number of sharks/day preceding (week prior)	Mean sharks/day week following event	Mean number of sharks/day preceding (week prior)	Mean sharks/day week following event
Killer whale predation	2/2/2015	69	8.25	0	0	0
White shark mortality	29/10/2023	4	4.67	1	4.14	0.16
Killer whale sighting	27/10/2024	5	1	1.28	0.63	0.14

commercial vessels operating in the region. We also recorded instances of killer whale presence or of likely dead white sharks at the Neptune Islands, which did not result in prolonged absences. For example, the sighting of an adult male killer whale on 27 October 2024 led to a short absence of 5 days prior to white sharks returning and being sighted again (Fig. 2, Table 2). In addition, other organisations tagged white sharks internally as part of several white shark research programs, which could also be detected by our acoustic receiver. An internally tagged white shark is suspected to have died on 29 October 2023 on the basis of continuous detections at one of the Neptune Islands receivers. This carcass could have triggered some avoidance by other white sharks, for example, through the release of necromones (Stroud *et al.* 2014). Yet, it resulted only in a short 4-day absence and a slight decline in abundance (Fig. 2), indicating that the presence of a deceased shark does not necessarily trigger prolonged absences.

Animals experience varying levels of predation risk as they navigate heterogeneous landscapes, and behavioural responses to perceived risk can structure ecosystems (Gaynor *et al.* 2019). In the ecology of fear, a predator depletes a food resource by frightening rather than killing all its prey (Brown *et al.* 1999), potentially producing downstream density-dependent effects. The role of fear and complex interplay between killer whales, white sharks, and seals has been documented between white sharks and seals, and killer whales and white sharks (Laroche *et al.* 2008; Towner *et al.* 2022). However, limited work has attempted to account for the white shark being both seal predator and killer whale prey or has assessed the relative contribution of fear versus resource distribution in shaping the patterns of white shark habitat use. With the appearance of killer whales, fear is incorporated into white shark decisions to either remain and continue to hunt for high-calorie prey under the risk of predation or move to avoid being hunted. At the Neptune Islands, the short and rare visits from killer whales is unlikely to lead to prolonged absences by white sharks as the risk of being predated on is low, and there are more benefits to gain from accessing high-calorie prey. Alternatively, limited exposure to killer whales has not yet led to white sharks learning of the predatory risk from this species, nor resulted in predatory avoidance behaviour. In contrast, white sharks might benefit from leaving the Neptune Islands and visit different colonies to reduce seal alertness that would otherwise occur from being continuously exposed to potential predation. In conclusion, although killer whale predation can prompt acute behavioural responses as observed in other regions, it is unlikely to be the sole or dominant driver of the white shark long-term absences at the Neptune Islands. Future research should move beyond the focus of displacement from killer whales locally and consider other factors and the broad ecological context to understand what drives white shark displacement and prolonged absences.

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Conflicts of interest. C. Huveneers and L. Meyer are Guest Editors for the collection 'White Sharks Global proceedings and recent advances in white shark ecology and conservation'. To mitigate this potential conflict of interest, they had no editor-level access to this paper during peer review. The authors have no further conflicts of interest to declare.

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