Ocean warming increases residency at summering grounds for migrating bull sharks (*Carcharhinus leucas*)

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HIGHLIGHTS

- Migrating bull sharks have increased residency at summering grounds off Sydney, Australia by on average 1 day per year over a 15-year period
- Sharks showed high individual variability across years but increasing trends persist and males had longer seasonal residency than females, yet females varied more over the years.
- SST data showed an increase in mean ocean temperatures off Sydney by up to 0.67°C, in parallel to prolonged bull shark residency which increases overlap with prey and people

GRAPHICAL ABSTRACT
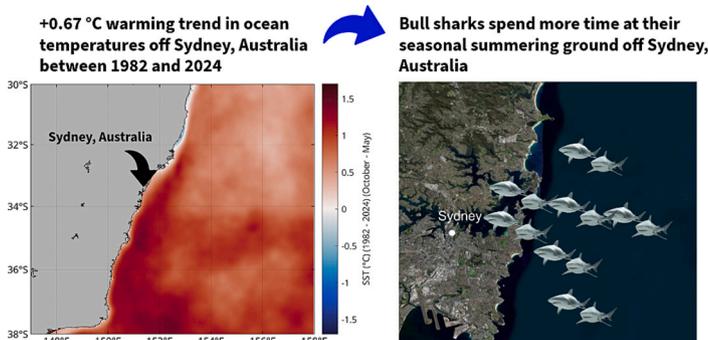
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ABSTRACT

Globally, climate change is driving warming ocean temperatures, increasing the frequency and severity of extreme temperature events and altering current systems. Consequently, distributions and movement patterns of marine species are shifting, causing changes to ecosystem functioning. Migration patterns of large-bodied species are also expected to be affected by climate change. However, contemporary evidence of such changes to the spatio-temporal dynamics of movement and residency in migratory marine predators is rare, consisting mainly of predictions of distributions under future climate change scenarios because long-term tracking/catch data is difficult to obtain. Here, we use passive acoustic telemetry data spanning 15 years (2009–2024), in combination with remotely sensed and in-situ temperature data, to investigate how shifts in climate influence residency duration and migration timing in migratory bull sharks (*Carcharhinus leucas*) on their temperate summering grounds. Our results show that sharks have delayed departure from their temperate summering grounds off Sydney, Australia by an average of 1 day per year over a 15-year period, while also for the first time recording

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arrival times in October rather than November, as previously published. As a result, sharks are increasing residency duration, shifting the timing of migrations back to tropical latitudes for the colder months. Bull sharks depart temperate summering grounds upon possible long-term exposures to temperatures of ~19–20.5 °C and below. Increases in sea temperatures are likely reducing the species' exposure to this thermal limit. In concordance, we found an average warming of 0.67 °C based on remotely sensed sea-surface temperature data (1982–2024) and of 0.57 °C based on in situ data (2006–2024) at our study site. As bull sharks are high-trophic level predators and implicated in shark-human interactions, more time spent at temperate summering grounds has the potential to impact local ecosystems through intensified predation pressure, while increasing temporal overlap with people in estuarine and coastal areas.

1. Introduction

Across terrestrial and marine ecosystems, seasonal environmental changes, such as in temperatures, light availability, winds and ocean currents cause alterations in local resource availabilities, which has profound impacts on the distribution and movement of animals leading to substantial temporal changes in local biomass (Gordo, 2007; Avgar et al., 2013; Riotte-Lambert and Matthiopoulos, 2020). This seasonal shift of biomass is responsible for changes in local predation pressure, competition and community structure (Bauer and Hoye, 2014).

Animal migration is one of the most conspicuous of such shifts (Dingle, 2014). The associated, often annually re-occurring movements, take place on a variety of scales, ranging from seasonal long-distance migrations of baleen whales (Geijer et al., 2016) to the overwintering movements of frogs within wetlands (Semlitsch, 2008). Given that the spatio-temporal dynamics of seasonal shifts in animal biomass are intricately linked to seasonal environmental patterns (Avgar et al., 2013; Shaw, 2016; Lubitz et al., 2022), mounting evidence suggests that anthropogenic climate change is severely impacting these dynamics (e. g., Malcolm et al., 2002; Robinson et al., 2009; Visser et al., 2009; Shaw, 2016).

Despite recent advances in our understanding of the effects of climate change on species distribution and movements in marine ecosystems, knowledge still lags behind that of terrestrial counterparts (Pinsky et al., 2020). Persisting knowledge gaps represent a critical weak point in our capacity to accurately predict and anticipate climate change impacts on marine ecosystems. This is concerning given the fact that marine species demonstrate range shifts six times faster than terrestrial species (Pinsky et al., 2020; Gervais et al., 2021).

An increasing body of work over the last 20 years has illustrated the severe impacts that rises in the frequency and intensity of marine heatwaves can have on community structure, species distribution and critical ecological links (Harley et al., 2006; Doney et al., 2012; Smale et al., 2017; Smale et al., 2019; Gervais et al., 2021). Furthermore, the tropicalisation of high latitude ecosystems, through a rise in mean ocean temperatures and changes in ocean current dynamics, is causing complex range expansions and contractions which may result in major restructuring of ecosystems, through novel species interactions (e.g. Cheung et al., 2012; Vergés et al., 2014; Smith et al., 2021).

Despite the likely extent of the problem, direct evidence of range shifts, habitat use and changes to community structure is mainly restricted to small-bodied, sessile and habitat-forming species, or species with small, defined home ranges. This is due to the fact that they are logistically easier to sample and observe in the repeated, systematic way necessary to accurately determine range shifts (Gervais et al., 2021; Davis et al., 2023). For large bodied and highly mobile species, occurring at lower densities, especially pelagic fish and elasmobranchs (sharks and rays), most work to date has focused on predicting shifts in ranges and migratory patterns under future climate change scenarios by combining environmental observations with presence/absence datasets (Pikesley et al., 2015; Champion et al., 2018; Niella et al., 2020, 2022a). Direct observations of shifts in the distribution and migration patterns of large predatory sharks in response to climate shifts that are already occurring are less common (but see Chaudhary et al., 2021;

Hammerschlag et al., 2022; Matich et al., 2024). Given the critical roles in shaping wide-ranging ecosystem processes through predation and nutrient transfer/risk effects (Heithaus et al., 2012; Barnett et al., 2017), as well as public safety considerations (Barnett et al., 2022; Smoothey et al., 2023), assessments of contemporary shifts in the distribution and migratory behaviour of large, mobile shark species are needed.

The bull shark (*Carcharhinus leucas*) is a large-bodied, highly mobile marine predator that exhibits complex yet predictable movement patterns across its distribution (Heupel et al., 2015; Lea et al., 2015; Espinoza et al., 2021; Lubitz et al., 2023a, 2023b). Individual adult bull sharks adopt different movement strategies where some are residents in subtropical and tropical areas while others are highly migratory and regularly move between tropical latitudes in winter and temperate habitats in summer with some individuals travelling up to 6000 km a year (Daly et al., 2014; Heupel et al., 2015; Lee et al., 2019; Smoothey et al., 2019; Espinoza et al., 2016; Lubitz et al., 2023a, 2024; Barnett et al., 2024). These re-occurring, annual migrations to temperate summering grounds make them a useful model species to investigate contemporary evidence for the impacts of climate change on migration patterns in mobile marine predators.

In Australia, bull sharks are the target of state-operated shark control programs due to implications in shark-human interactions (West, 2011; Tate et al., 2021; Tucker et al., 2022; Riley et al., 2022), including at one of their summering grounds; the coastal areas around Sydney, Australia's largest city (Smoothey et al., 2016). The broader south-east coast of Australia has been deemed a climate change hotspot, with some of the most rapid warming rates of ocean temperatures in the world (Gervais et al., 2021). Bull shark distributions have been forecast to extend further south under future climate change scenarios with changes in migration behaviour likely to occur (Niella et al., 2020). However, contemporary evidence for such changes to regular, annual movement patterns are rare (Smoothey et al., 2023; Matich et al., 2024).

In this study, we use 15 years of acoustic tracking data from 92 migratory sharks to investigate if migration timing and residency patterns of bull sharks in and around Sydney Harbour, a highly urbanised estuary, have increased over this period. We also analyse long-term temperature data for the region to establish a link between residency times and a potential rise in seasonal, mean ocean temperatures.

2. Methods

2.1. Study area and acoustic array

The study area includes the entry to Sydney Harbour (ca. 33°51′S, 151°14′E), in New South Wales (NSW), Australia which is a large, heavily urbanised estuary. It is approximately 30 km long with a maximum width of 3 km. Outside of the estuary, the study area comprises the coastal area 24 km to the south and extends 24 km offshore (Fig. 1). The entrance to Sydney Harbour is approximately 2.4 km wide and since 2009 four Innovasea™ acoustic receivers have been deployed at depths between 25 and 29 m and placed approximately 450 m apart. This arrangement of receivers with overlapping detection ranges effectively acts as a gate, detecting any acoustically tagged animals either side of the gate (Fig. 1). Additionally, up to 30 Innovasea™ acoustic

receivers were deployed during the study period in a straight, inshore-offshore line from Bondi Beach. Again, receivers were approximately 450 m apart, so detection ranges are overlapping to detect acoustically tagged animals moving latitudinally along the coast (depth range: 20–120 m) (Fig. 1). The Bondi line was reduced in year five of the study (2013/2014) to only include the 15 most inshore receivers. Annual receiver deployments, maintenance and data offloads are managed by the Integrated Marine Observing System (IMOS, 2025) animal tracking facility, a national, public database for acoustic telemetry data. This coastal area has been shown to be a summering ground for adult and sub-adult bull sharks along the Australian east coast (Smoothey et al., 2016, 2019; Lubitz et al., 2024) and provides an opportunity to evaluate the effects of climate change on bull shark residency given the long-term receiver deployments, coupled with known occurrence and residency of bull sharks in this region. Here, bull sharks are usually present between November and May, the Austral warm water period, although they vary in abundance and residency times throughout this period (Smoothey et al., 2016, 2019, 2023; Lee et al., 2019). Outside of this period, bull

sharks are largely present in the subtropical and tropical areas of Queensland (Heupel et al., 2015; Lee et al., 2019; Lubitz et al., 2023b; Smoothey et al., 2023).

2.2. Acoustic tracking and data collection

Between March 2009 and May 2024, 327 sub-adult and adult bull sharks were fitted with V16-6 L high-powered Innovasea™ acoustic transmitters in coastal regions of NSW and QLD. Transmitters were programmed on a pseudo-random repeated rate ranging from 30 to 90 s and 40–80 s with an estimated battery life of 10 years (for detailed tagging methods see Smoothey et al., 2019, 2023; Barnett et al., 2022; Lubitz et al., 2023b). Out of those, 92 individuals (32 females, 60 males, 168–320 cm, mean = 258.71 ± 38.96) were detected on the Sydney Gate and Bondi Line receivers between 2009 and 2024. During our monitoring period, bull sharks were detected within the study area between October–May, hence we split all acoustic detections into "bull shark years" rather than calendar years. For example, all acoustic
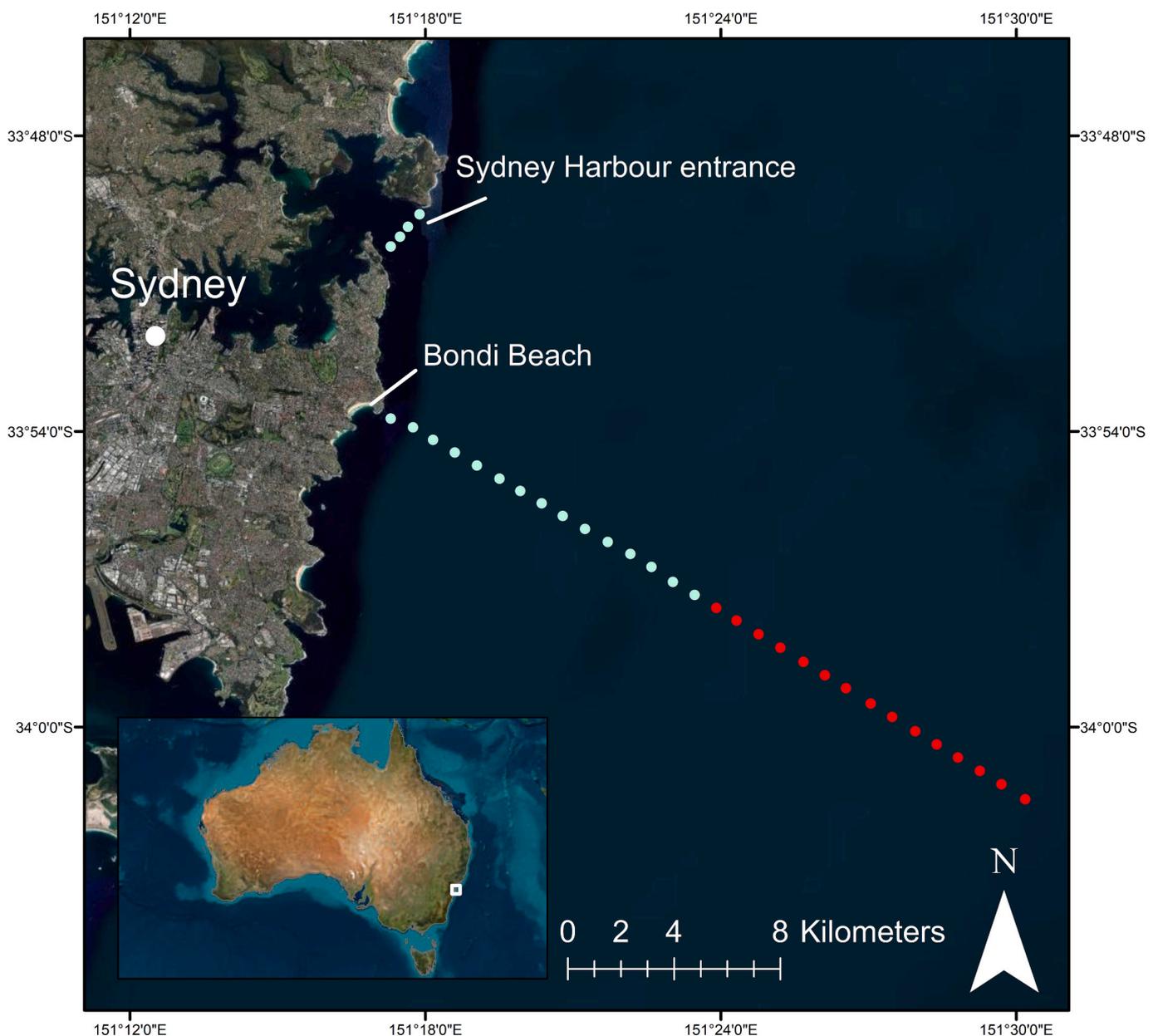

Fig. 1. Map showing the study area around Sydney, on the Australian south-east coast. Circles represent acoustic receivers. White circles are receivers deployed throughout the whole study period and red circles are receivers that were removed after five years (2013/2014).

detections registered from October 2023 until May 2024 were part of year 15 with a total study period of 15 years (2009–2024). During this period, the earliest a bull shark arrived in Sydney was October 18th 2020 and the latest a shark departed was May 24th 2013. Hence, October 18th to May 24th was considered as the maximum extent of the bull shark season for each year. Note, one individual was only detected in the Sydney area once, on July 3rd 2022, well outside the usual bull shark season and was removed from formal analyses as an outlier. From this, we determined the arrival and departure dates in the study area for each shark across years and used number of days that passed between these dates to generate a departure index (see Matich et al., 2024 for a similar approach). For example, if a bull shark was last detected at either gate on May 24th in a given year, the departure index for this shark in that year would be 220 days. All tracking data processing was performed in the statistical software R (R Core Team, 2024).

Next, we extracted ocean temperatures for our study period from IMOS moorings which collect hourly data across several depths between the surface and 69 m, approximately 2 km offshore from Bondi Beach (attached to a receiver along the Bondi line) using the remora R package (Jaine et al., 2021). For detailed information on the mooring metadata, see Roughan et al. (2010). To facilitate later comparisons with remotely sensed long-term sea surface temperature (SST) data and because bull sharks mainly occupy waters <40 m depth at their range limits (Lee et al., 2019; Lubitz et al., 2024), we filtered the mooring data to <40 m to calculate daily mean temperatures. Note, this mooring had a data gap between January 7th 2009 and December 28th 2010. To investigate a direct impact of temperature on bull shark departure from the study area, we extracted mooring data for the 7 days prior to each shark leaving the Sydney area for a given year, including the day of departure, to create a variable representing mean temperature prior to departure.

2.3. Data analysis

We used a generalised linear mixed model (GLMM) with a gaussian distribution to investigate the impact of year, mean temperature of the week prior to departure and sex, on bull shark residency patterns in the Sydney area. Models were constructed using the glmmTMB R package (Brooks et al., 2017), where the index of departure (i.e., the day of departure during a "bull shark year") was used as the response variable and year, sex and the mean temperature of the 7 days prior to departure (including day of departure) were included as predictor variables. Individual shark ID was included as a random factor to account for repeated measures of the same individuals and individual behavioural variability. Variables were tested for normality, linearity and homoscedasticity. Initial data exploration revealed apparent non-linearity in the temperature prior to departure variable. Thus, we fitted the model, including a quadratic term for this variable. Model fit was inspected for both, a variant with and without the quadratic term with diagnostics provided in the DHARMa R package and the final models were compared using the Akaike Information Criterion (AICc) (Hartig, 2024). During initial data exploration, we found no apparent trend for arrival index in the study region over time, and thus did not model arrival index as a response variable.

To provide further insights into bull shark thermal preferences, we accessed all bull shark detections across receiver stations along the entire Australian east coast from the IMOS database, including individuals not detected in our study region to build a species thermal distribution. These were filtered to daily detections per individual and receiver station. Then, we accessed the jplMURSST41 SST data set from the ERDDAP server through the rerddapXtracto package in R (Mendelssohn, 2019). This L4 satellite data set provides daily SST data at a resolution of 0.01° and can easily be amended to acoustic telemetry data via the rerddapXtracto R package. For each day and for each receiver station a shark was detected on, we extracted the corresponding temperature value from the jplMURSST41 data set. All values were combined into a coast-wide species thermal range for bull sharks.

A spatial trend analysis for ocean temperatures over southeastern Australia (including at the point of the IMOS mooring off Bondi Beach) was done using the Level-4 OSTIA SST (5 km resolution) dataset from January 1982 to December 2024 (43 years), as well as during the period of the deployment of the IMOS mooring (June 2006–May 2024). For this analysis the OSTIA SST was chosen due to its long-term data availability. The overall trends were estimated using the Theil-Sen estimator. The estimator is non-parametric and hence more robust than parametric least-squares regression because it is resistant to outliers and does not draw from any probability distribution. Theil–Sen uses the median to estimate the slope, as opposed to least squares, which makes use of a weighted mean for slope estimation. Spatial SST trends were calculated using each grid point within the designated area of the gridded SST product. In addition, the SST and mooring data trends were calculated using anomalies to avoid the complicated effects of seasonality on the trend values. Ostia SST trends in the region were validated via the IMOS Bondi mooring using the same time period and eliminating the mooring gap readings within the SST product (January 7th 2009–December 28th 2010). Validation and trends were obtained by converting all products into monthly data during bull shark years. Additionally, the average depth of the shallowest temperature logger on the mooring was 15.3 m during the duration of the deployment with it's shallowest and deepest depths being 12.5 m and 21.44 m, respectively. Data from these shallower depths were used to compare to the trends in the OSTIA SST product. This was done via MATLAB R2023a.

3. Results

From 2009 to 2024, 92 acoustically tagged bull sharks consisting of 32 females and 60 males (168–320 cm, mean = 258.71 ± 38.96), registered 55,730 individual detections on the Sydney Gate and Bondi Line receivers between October and May (Fig. 2). Forty-six individuals were detected during more than four years, and out of those, seven sharks were detected on eight or more years and two individuals were detected during 10 years in total (Fig. 2). Based on previous literature using the same data set until 2018, the earliest bull shark detection in our study region for a given year was in November (Lee et al., 2019; Smoothey et al., 2019; Espinoza et al., 2016, 2021; Niella et al., 2022b). However, we report for the first time, bull sharks arriving in the Sydney region during the month of October on three occasions (two in 2020 and one in 2023), extending the period bull sharks are detected in the area. However, no clear trend was observed in arrival times during our study period.

"Bull shark year" 10, spanning the October 2018–May 2019 calendar years, had the highest number of individual sharks detected in the study area with 34 animals registering detections (36.9 %) (Fig. 2). In contrast, "bull shark year" one, spanning the October 2009–May 2010 (Year 1) had the fewest number of tagged/detected sharks (*n* = 2, 2.2 %). Due to this low number of tagged sharks compared to other years (mean = 23.7 ± 8.4), 2009–2010 was removed from further analysis. This reduced the number of sharks included in our study to 90, yielding a total of 347 departure indices.

On average, the time between first and last detection for bull sharks in the Sydney region, in a given bull shark year, was 61.2 days (SD ± 40.5 days). While some sharks were detected for one day only within the area, others had detections spanning up to 197 days in a given "bull shark year". Bull sharks were only detected on six of the 15 acoustic receivers located furthest offshore in the Bondi line (Fig. 1). This composed 0.6 % of total detections during the period these receivers were deployed, suggesting the removal of the 15 offshore receivers had negligible impact on results (Fig. 1).

Based on the AICc, the best fitting GLMM was the model including bull shark year, sex and the quadratic term for mean water temperature in the week prior to each shark's departure. There was a significant positive trend in the departure index over time (*p* = 0.008, Fig. 3A). Between year two (2010/2011) and year 15 (2023/2024) bull sharks
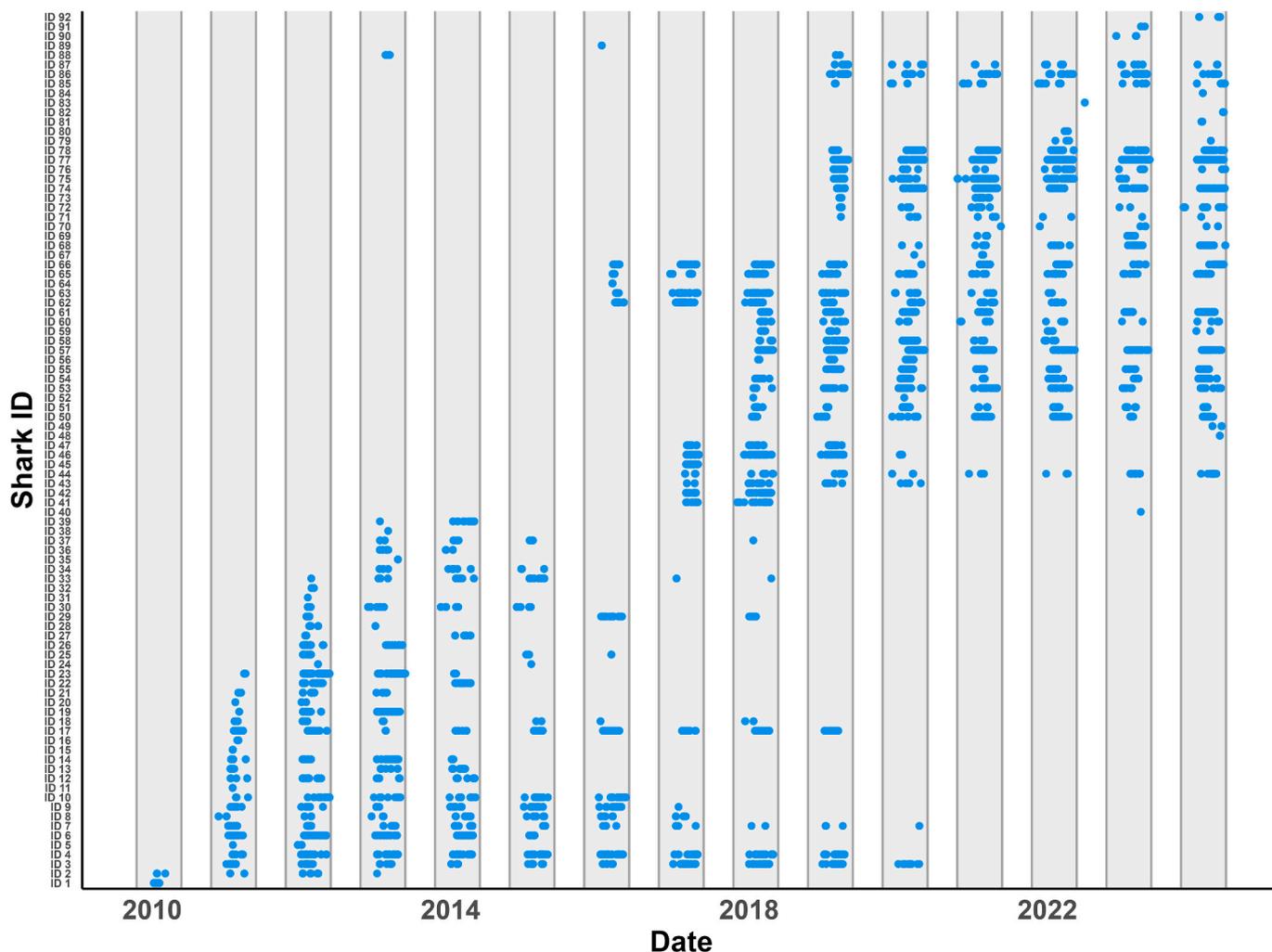
Fig. 2. Combined presence/absence plot of acoustically tagged bull sharks detected by the Sydney Gate and Bondi Line receivers between 2010 and 2024. Each line on the y-axis represents an individual shark. Blue dots indicate registered detections while the grey-shaded areas delineate "bull shark year", each being a period from October 18th in one year and May 24th of the following year.

delayed their departure from their summering grounds, by an average of ~15 days; at a rate of ~1 day per year. At the beginning of the study period, the last detection in the vicinity of Sydney was on average on the 26th of March (index = 160 days), by the end of the study period, this was delayed on average until 12th of April (index = 175 days).

The mean water temperature in the week prior to each shark's departure, including the day of last detection, also had a significant effect on departure index (Fig. 3B). Here, both a first order and a second-order polynomial term for this variable were required to best capture the nonlinear trend in the data (Fig. 3B). Departure index increased initially with increasing mean temperature, but this trend began to slow at ~20 °C after which it plateaued and dropped slightly, suggesting no indication that temperatures experienced within the week of departure above ~21 °C would have further increased the departure index.

On average, male bull sharks departed 21 days later than females (Fig. 3C). Additionally, females had higher variability in departure index than males (Fig. 3C). Overall, the GLMM including the quadratic term, had a marginal R^2 of 0.23 and a conditional R^2 of 0.41, indicating that individual variability accounted for almost half of the explained variance.

The acoustic detections from the east coast of Australia used to build a coast-wide thermal range for bull sharks yielded 192,317 daily temperature records (Fig. 4). This was based on shark detections from April 2009 to January 2025, from 348 individuals that occupied areas

between latitudes 11.42°S in tropical QLD and − 36.9°S in southern NSW, spanning approximately 2900 km straight-line distance (Fig. 4). This thermal range was generated to situate the mean temperature prior to departure from the Sydney area in a broader thermal context, for this species across it's east coast distribution. The 5th percentile of this thermal range was 20.5 °C, the 2nd percentile was 19.8 °C and the 1st percentile was 19.4 °C, while the lowest SST value from the jplMURSST41 data set associated with a bull shark detection was 16.6 °C. In agreance with such lower temperature thresholds, in March 2021 five bull sharks had their last detections in the Sydney Harbour region within 3 days of each other, which coincided with sea temperatures at the mooring as low as 16.5 °C. This resulted in mean temperatures of the 7 days prior to departure for those sharks to fall between 18.7 °C and 20.6 °C, and mean daily temperatures of the day of departure to be between 16.6 °C and 19 °C.

Analysis of linear spatial Theil-Sen estimator trends reveals a prevalent warming pattern across the study area during both the extended (1982–2024) and recent (2006–2024) periods in the OSTIA SST data set (Fig. 5). A notable exception to this general warming trend is observed along sections of the northern coastline, where a cooling trend is evident in the longer period (1982–2024) or a neutral trend is noted in the shorter period (2006–2024) (Fig. 5). Furthermore, the warming trend exhibits spatial heterogeneity, with a more pronounced heating trend concentrated south of approximately 32°S, extending offshore to
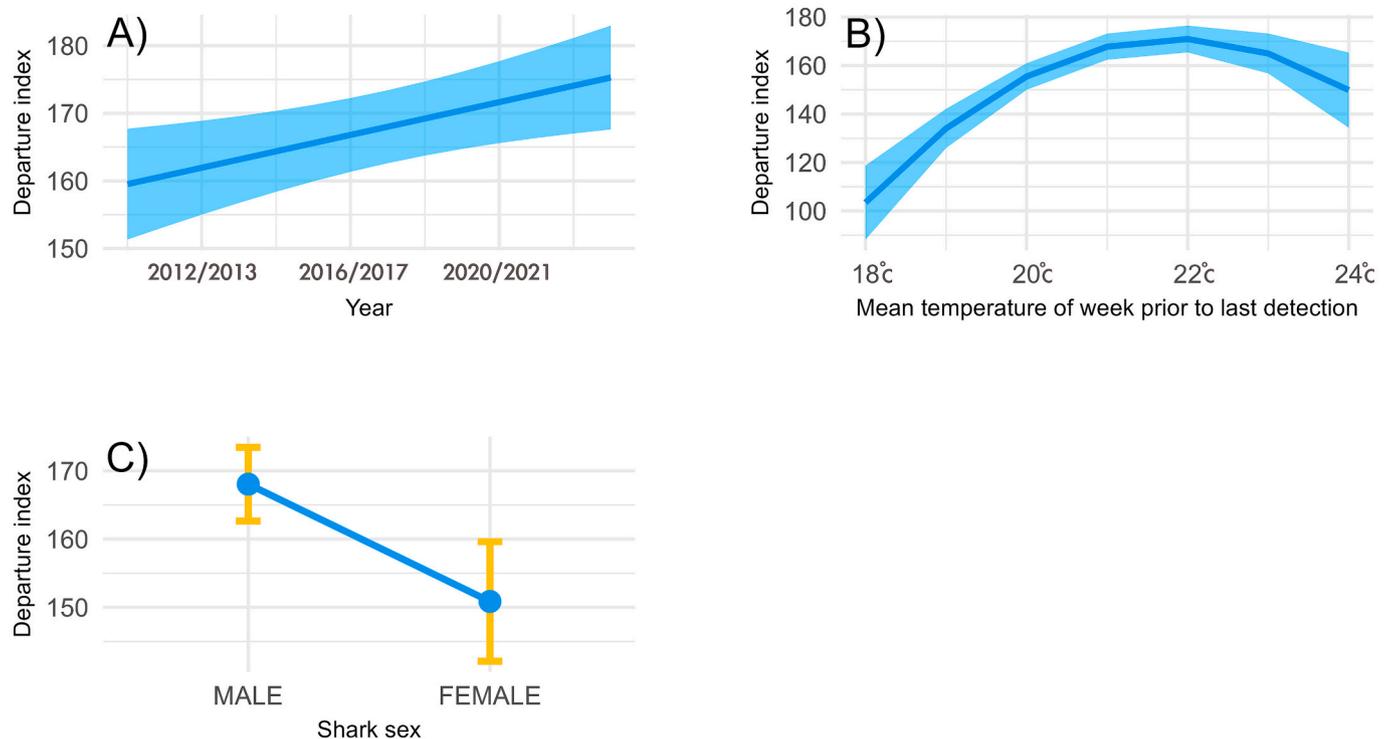
Fig. 3. A) Trend in departure index, i.e. which day within a bull shark year bull sharks left from the Sydney area over the 14-year monitoring period, B) the influence of mean temperature during the week prior to last detection in the Sydney area on departure index and C) the influence of bull shark sex on departure index.

approximately 34°S, during both timeframes.

The Level 4 OSTIA (SST) product trend was validated against data from the IMOS Bondi mooring (Fig. 6A). Although a substantial data gap existed in the IMOS Bondi mooring data (January 7th 2009–December 28th 2010), its impact on the overall temperature trend derived from the OSTIA SST dataset between 2006 and 2024 (October–May) was assessed as negligible (Fig. 6A). Specifically, removal of the OSTIA SST data corresponding to the mooring gap resulted in a trend difference of <0.03 °C. Therefore, we posit that a complete Bondi IMOS mooring dataset, devoid of gaps, would yield a total trend that is negligibly different from the trend calculated with the existing data gap. The total trend (October–May) from 2006 to 2024 at the Bondi mooring site was +0.57 °C, whereas the corresponding OSTIA trend was +0.32 °C (Fig. 6A). Over the longer period for which data were available (1982–2024), the OSTIA-derived trend was +0.67 °C. Similar to the increasing trend in water temperature anomalies during the October–May period each year in the OSTIA data set (1982–2024) and at the Bondi mooring (2006–2024), the mean annual length between first and last detection (in days) of bull sharks at our study site increased during the monitoring period (Fig. 6B).

4. Discussion

Global climate change is having diverse impacts on marine ecosystems (Poloczanska et al., 2016; IPCC, 2023). Rising mean temperatures and increases in the severity and frequency of extreme temperature events are driving large-scale alterations to ecological communities and the spatial distribution of marine organisms (Champion et al., 2021; Gervais et al., 2021; Holland et al., 2021; Lubitz et al., 2024). In particular, south-east Australia is experiencing accelerated warming and is deemed a "climate change hotspot" (Wu et al., 2012; Hobday and Pecl, 2014; Gervais et al., 2021). Here, warming of ocean temperatures and oceanographic changes in the East Australian Current have already resulted in range contractions of temperate species, poleward expansions in tropical species and changes to fisheries yields (Suthers et al.,

2011; Kingsbury et al., 2020; Gervais et al., 2021; Schilling et al., 2022).

Using long-term telemetry data with individual tracking times of up to 10 years, we show that large, migratory bull sharks have on average delayed departure from their summering grounds in temperate waters off Sydney, Australia by ~1 day per year between 2010 and 2024. Additionally, we report for the first time, bull sharks arriving in the Sydney region during the month of October on three occasions (two in 2020 and one in 2023), whereas in previous studies using the same data set but only until 2018, bull sharks arrived no earlier than November (Smoothey et al., 2019; Lee et al., 2019; Espinoza et al., 2021; Niella et al., 2022b).

These earlier arrivals and later departures are in parallel with an average warming of 0.67 °C in water temperature based on the OSTIA SST data set (1982–2024) and 0.57 °C based on the Bondi mooring data (2006–2024) during the annual period of bull shark presence (October–May) in this region. Similarly, Matich et al. (2024) also found that juvenile bull sharks have delayed their annual migration from estuaries along the Gulf of Mexico at a rate of 0.75 days per year between 1981 and 2021 in response to climate change. The delay of return migrations to subtropical and tropical areas for winter and thus extended stays on summering grounds observed here, confirm previous predictive work forecasting an increase in suitable year-round habitat for bull sharks and tiger sharks (*Galeocerdo cuvier*) towards higher latitudes along the Australian east coast under future climate change scenarios (Niella et al., 2020, 2022a).

Across ectothermic species, maintaining an optimal body temperature is crucial for physiological function and growth (e.g., Donley et al., 2007; Wheeler et al., 2021). For example, tiger sharks can occur across a wide range of temperatures, but abundance and physiological performance are highest around 22 °C (Payne et al., 2018). Although adult bull sharks can sustain temperatures under 19–20 °C during brief dives or short-term upwelling events, prolonged exposure to temperatures below this range appear to initiate emigration from summering grounds in and around Sydney Harbour (Smoothey et al., 2019), resulting in lower departure indices, similar to observations in South Africa (Lubitz et al.,
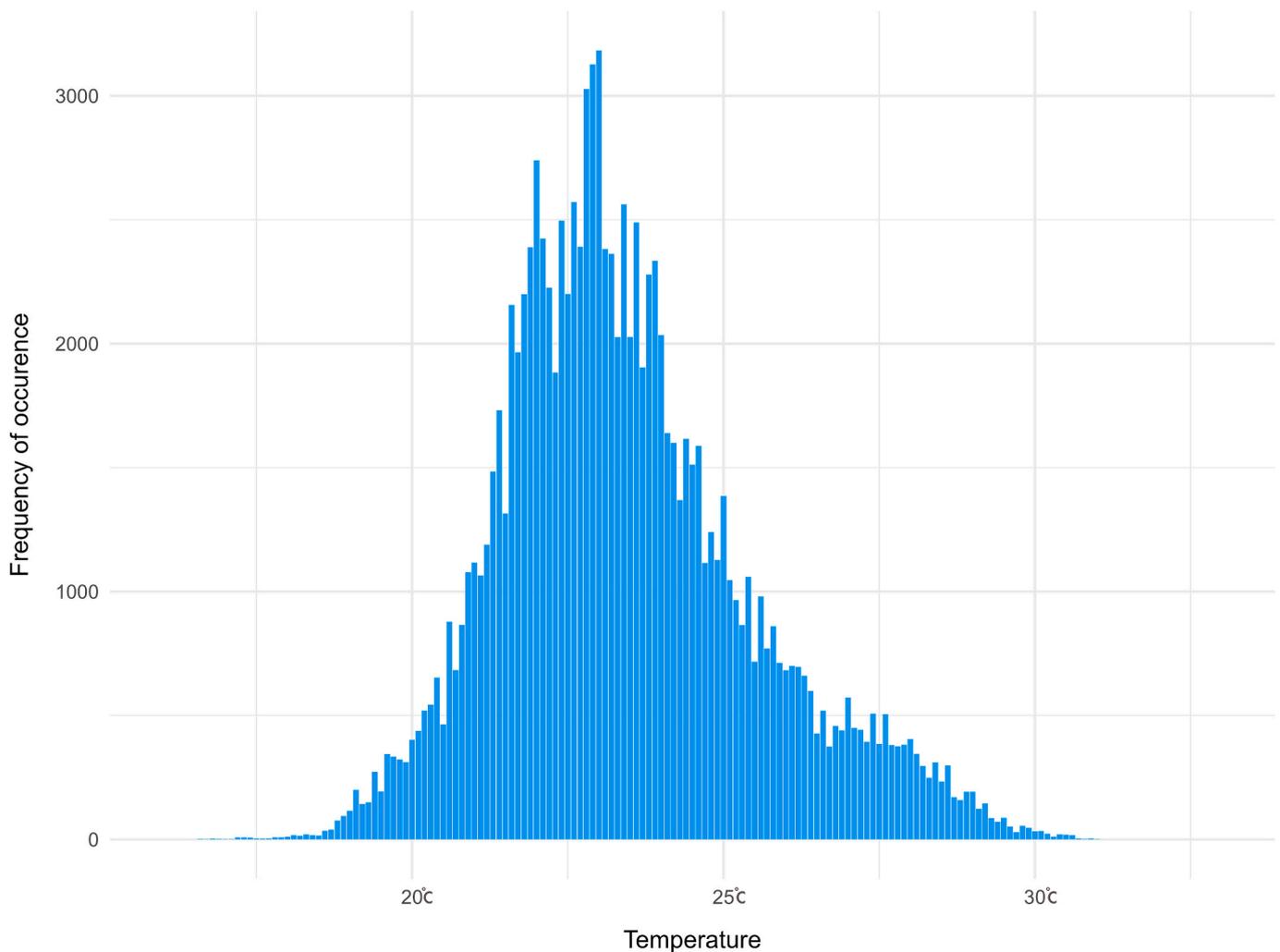
Fig. 4. Histogram for the thermal range of bull sharks along the Australian east coast based on 192,317 acoustic detections.

2024). This is further exemplified by the five sharks that were last detected in our study region within three days of each other during the 2020/2021 season, coinciding with temperature drops at the coastal mooring to as low as 16.5 °C. It should be noted that bull sharks can occur well within the Sydney Harbour estuary, which despite being well flushed by oceanic waters at its entrance, experiences generally smaller temperature fluctuations than nearby coastal waters (Johnston et al., 2015).

Temperatures below 20.5 °C are within the 5th percentile of the thermal range for adult bull sharks along the Australian east coast and previous studies in South Africa and Sydney Harbour have demonstrated that catches and acoustic detections of tagged animals are extremely rare in temperatures below 19 °C (Smoothey et al., 2016; Smoothey et al., 2023; Lubitz et al., 2024; Daly et al., 2025). In fact, bull shark fatalities due to intense, rapid and/or long-lasting temperature drops of up to 9.2 °C in <24 h, associated with upwelling have been recorded in South Africa (Lubitz et al., 2024). Combined, this confirms a possible long-term temperature threshold of ~19–20.5 °C for adults of this species.

During the annual period that bull sharks were detected in our study area (October–May), daily mean temperatures measured at the mooring ranged between 15.4 and 25.7 °C and fluctuated within this range throughout the season. It appears that if sharks can maintain a threshold over ~20 °C, without long term exposure to lower temperatures, the departure index does not increase substantially. This indicates that it is not the warming temperatures in our study area per se that increase

residency times in a gradual manner. Rather, a likely decline in the occurrence of temperatures below ~20 °C between October and May over the last four decades associated with average warming may allow sharks to increase avoidance of sub-optimal temperatures and thus remain longer at their summering grounds. Although removed from formal analysis, one individual was detected in July, indicating that possible suitable thermal windows in our warm temperate study area might become more available throughout the year.

Behavioural thermoregulation by exploiting varying habitats and depth gradients is a key driver for the spatial distribution and fine-scale behaviour of many elasmobranchs and impacts foraging behaviour and reproduction (Speed et al., 2012; Thums et al., 2013; Sulikowski et al., 2016; Watanabe et al., 2021). For example, small-spotted catsharks (*Scyliorhinus canicula*) forage in shallow, warmer waters, while resting in deeper cooler environments to optimise foraging and digestive activity (Sims et al., 2006). Similarly, pregnant female tiger sharks appear to seek out shallow, protected, warm habitats suitable for successful gestation (Sulikowski et al., 2016). Reproduction is an unlikely driver for bull shark movements to summering grounds as mating and parturition have not been documented there (Smoothey et al., 2016). Yet, our model results demonstrate a significant difference between males and females in their departure index, where males departed later from our study area than females. This could indicate sex-specific constraints on migration to/from and residency at summering grounds, possibly linked to reproduction in coastal areas north of Sydney.

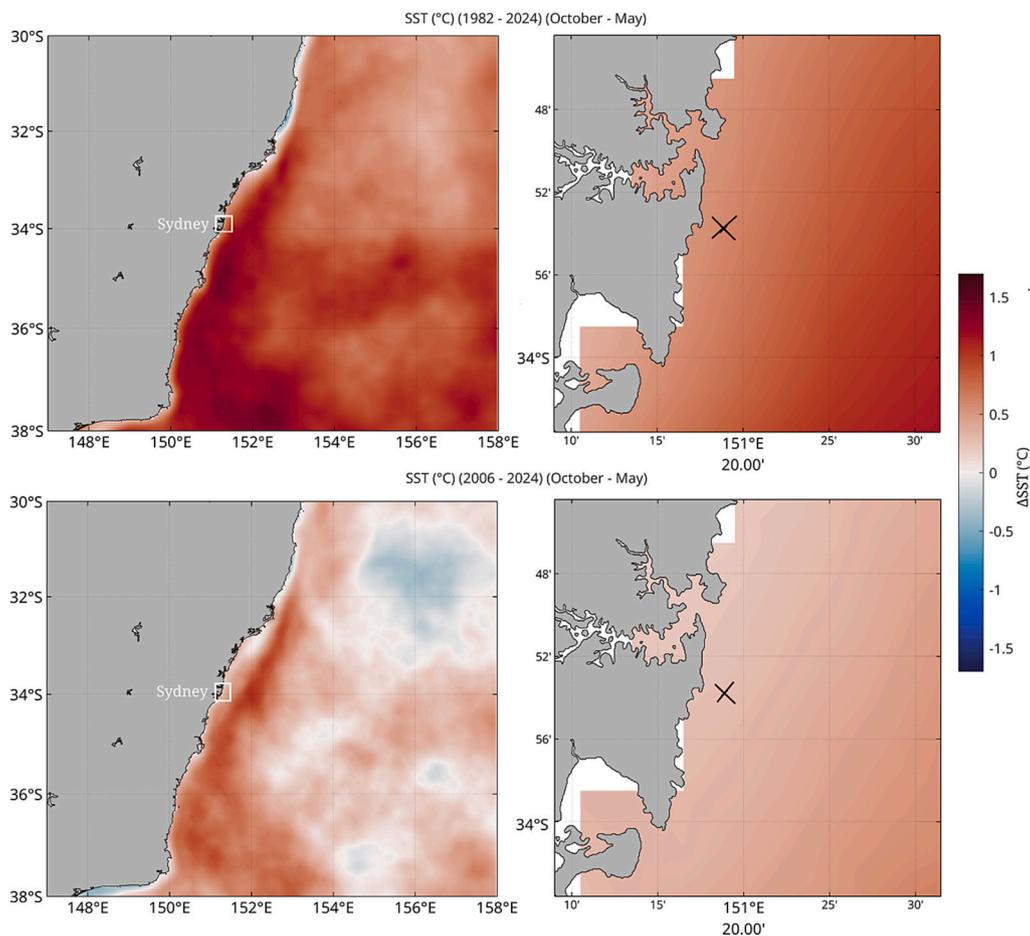The main driver for bull shark movements to summering grounds,

Fig. 5. Spatial trends for southeast Australia for 1982–2024 and 2006–2024 (October–May) from the OSTIA SST data set. White boxes indicate the zoomed-in area while the black crosses indicate the position of the Bondi IMOS mooring.

including the Sydney area, is thought to be linked to prey availability (Smoothey et al., 2016, 2019; Niella et al., 2022b; Lubitz et al., 2023a). Bull sharks likely time their presence with peaks in abundance and spawning activity of teleost prey which is highest during the warm season (Kingsford and Suthers, 1994; Neira et al., 1992; Niella et al., 2022b; Lubitz et al., 2023a, 2023b). In and around the Sydney Harbour estuary, bull sharks utilise fine-scale behavioural patterns to increase overlap in spatially complex habitats with prey species such as yellowfin bream (*Acanthopagrus australis*), silver trevally (*Pseudocaranx georgianus*) and mulloway (*Argyrosomus japonicus*) in response to environmental cues, including rainfall, while also possibly seeking out optimal temperature gradients (Smoothey et al., 2019; Smoothey et al., 2023; Lubitz et al., 2024). Although prey is the main incentive for migrations to summering grounds, temperature is the limiting factor as to when these resources can be seasonally accessed (Smoothey et al., 2016, 2023; Lubitz et al., 2023a, 2024). Yet, how climate change may alter distributions, movements and survival of prey at bull shark distributional limits and how this may further impact seasonal bull shark residency requires further research.

In the context of warming ocean temperatures in the study area, our observations support a resulting increase in residency time at summering grounds. Given a simultaneous poleward expansion of bull shark nurseries (Bangley et al., 2018; Mullins et al., 2024), it is probable that bull sharks may establish a greater presence throughout the year at their current summering grounds, if climate change driven warming of ocean temperatures continues at its present rate. Southward shifts of adult summering grounds are already occurring along the NSW coast (Smoothey et al., 2023).

In recent years, catches of bull sharks have increased in commercial fisheries and the shark control program along inshore areas of the NSW coast (Niella et al., 2020). However, it remains unclear if this is due to a general southward shift of bull shark populations, an increase in bull shark numbers due to a population increase, or both (Niella et al., 2020). Regardless of this, an increase in the number of high-level predators and prolonged, annual residency times in these temperate waters will likely have profound impacts on local ecological systems and people. Niella et al. (2022b) demonstrated complex seasonal predator-prey dynamics between bull sharks and teleost prey in Sydney Harbour. Increased predation pressure and competition with other predators has the potential to disrupt current ecological links and drive a decrease in survival rates for certain keystone species (Romero et al., 2018; Domenici et al., 2019; Peers et al., 2020). Future research to understand how increased presence of high-trophic level predators, such as bull sharks, in areas that are seasonally used, might affect local ecosystems is an important next step in marine climate change research.

Bull sharks are frequently implicated in depredation feeding on fish caught by commercial and recreational fishers before the catch is retrieved to the fishing vessel (Mitchell et al., 2018; Vardon et al., 2021; Griffin et al., 2022). A possible increase in residency times in temperate areas may be accompanied by a rise in depredation rates and add further pressure on local fisheries. Finally, bull sharks have been responsible for a number of bites on people (West, 2011; Tucker et al., 2022; Riley et al., 2022; Huveneers et al., 2024). Despite a relatively low risk of shark bites in NSW (0.6–3.3 per year^{-1}; Huveneers et al., 2024), the changes in the spatio-temporal dynamics of large bull shark occurrence at their summering grounds observed here implies increased time for sharks and
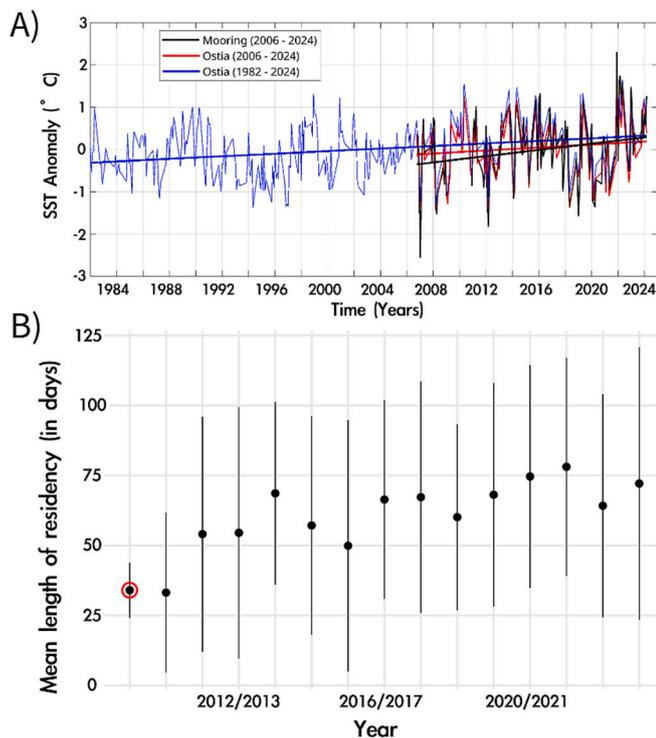
Fig. 6. A) Theil-Sen linear trends for the SST L4 OSTIA product (1982–2024), (2006–2024) and the Bondi IMOS mooring (2006–2024), B) The mean length of residency in days calculated from all sharks for a given year on the y-axis over time in the form of year on the x-axis. Again, year is summarised by bull shark season, lasting from October 18th until May 24th each time. The red circle highlights year one during which only two sharks were detected in the study area and which was subsequently removed from further analysis.

humans to potentially interact, especially given the high population density in and around coastal and estuarine areas of Sydney, which are otherwise characterised by the notable seasonal absence of bull sharks during the colder months (Smoothey et al., 2016, 2019, 2023). This study further supports current SharkSmart messaging about exercising caution in estuarine and coastal waters when water temperatures are above 19 °C (Smoothey et al., 2019, 2023).

In addition to prolonged bull shark residency potentially effecting local ecosystems and people, sharks may also be impacted through increased exposure to pollutants and other urban influences, as Sydney Harbour is a highly urbanised estuary adjacent to Australia's largest city. Sydney Harbour is affected by a variety of pollutants from urban runoff, including heavy metals (Stark, 1998; Johnston et al., 2015). However, if increased residency in the region could translate to a higher uptake of toxins in bull sharks remains unclear.

In summary, we demonstrate that migratory bull sharks are on average delaying their annual departure from their summering grounds around the coastal waters off Sydney by ~1 day per year, thereby increasing their residency times in this temperate region. An average warming of ocean temperatures likely results in reduced exposure of bull sharks to temperatures below preferred thresholds, allowing individuals to remain longer to exploit prey aggregations. This spatio-temporal shift in bull shark migrations along the NSW coast is likely going to impact local ecosystems and people, however, how exactly this may unfold remains unclear. This highlights the need for further research to evaluate the ecosystem effects and socio-economic impacts of climate-change driven shifts in distributions and migrations of this and other high-trophic level predators.

CRediT authorship contribution statement

Nicolas Lubitz: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Paul A. Butcher:** Writing – review & editing, Investigation, Data curation. **Patrick Vianello:** Writing – review & editing, Methodology, Formal analysis. **Adam Barnett:** Writing – review & editing, Investigation, Data curation. **Ross G. Dwyer:** Writing – review & editing, Investigation, Data curation. **Marcus Sheaves:** Writing – review & editing, Supervision, Investigation, Data curation. **Amy F. Smoothey:** Writing – review & editing, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing interests with regards to this manuscript.

Data availability

All data used in this manuscript are publicly available. Shark tracking and receiver meta data can be obtained from the Integrated Marine Observing System Animal Tracking Facility at https://animaltracking.aodn.org.au/. Temperature data from the IMOS mooring can be obtained via the Remora R package or from https://imos.org.au/ directly via the Australian Ocean Data Network. Remotely sensed SST data from the OSTIA data set can be obtained from the Copernicus Marine Service under the Ocean Products tab https://marine.copernicus.eu/.

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