Risky business: consistent breeding migration in a benthic shark despite environmental variability

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The timing of migration is essential for the survival and reproductive success of migratory species. Environmental and biological factors can influence the breeding success of these migrations. However, there is a lack of long-term studies on benthic migratory species that analyse their response to climatic variation. Climate change may threaten the breeding migration of species that rely on environmental cues to initiate migration. Port Jackson sharks, *Heterodontus portusjacksoni*, display high philopatry to their breeding grounds. Using passive acoustic telemetry, this study investigated the annual migration patterns of Port Jackson sharks at a breeding aggregation site in Jervis Bay, Australia. The influence of biological (sex and size) and environmental factors (temperature, East Australian current strength, rainfall, moon phase and period of the day) on these patterns was assessed over a 7-year period (2013−2019). The results of the linear mixed-effects models revealed annual and individual variability in migration timing, with males arriving and departing earlier than females. There was no influence of environmental variables on the migration timing of Port Jackson sharks. We found that more sharks arrived and departed at night. Overall, there was significant repeatability in migration timing for both arrival and departure. This interannual individual consistency has important implications for breeding success at the population level. Migration patterns that are unresponsive to environmental cues may lead to a mismatch between migration timing and suitable conditions for juvenile survival.

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Animal migration is often associated with broad-scale movements at two or more locations to reach profitable foraging grounds or suitable breeding areas (Luschi, 2013). Animals migrate as an adaptive response to increase their growth, survival or reproduction. However, migration comes with costs, including increased metabolic expenses. To minimize these costs, migratory species can adapt their migration timing to synchronize critical behaviours (foraging and reproduction) with ideal environmental conditions (Oestreich et al., 2022). For example, reproductive synchrony may maximize mating opportunities at breeding grounds and thereby ensure reproductive success (Hulthén et al., 2022). Both extrinsic (temperature and rainfall) and intrinsic factors (sex and size) can help species to time their migration (Dodson et al., 2020; Zenzal et al., 2023). For example, higher sea

surface temperatures can trigger earlier migration phenology in fish by altering their physiology (Sims et al., 2004; Volkoff & Rønnestad, 2020). However, anthropogenic climate change is altering several extrinsic factors (e.g. sea surface temperature) that could influence migration timing (Inouye, 2022). Migratory species may adapt to climate change by adjusting their migration timing, demonstrating phenotypic flexibility (Gabriel et al., 2005). For example, North American wood warblers (family Parulidae) change their arrival earlier for every 1 °C increase in spring temperature (Horton et al., 2023). Alternatively, if individuals rely on other cues to time their migration (e.g. social cues), they might maintain consistent migration timing regardless of ideal environmental conditions, resulting in a mismatch with important ecological events.

Elasmobranchs (e.g. sharks, rays and skates) migrate to return to their birthplace (natal philopatry) or birth region (regional philopatry) for parturition or breeding (Chapman et al., 2015). Sharks have slow life-history strategies, meaning that they are

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long-lived, slow-growing, reach sexual maturity late, have long reproductive cycles and produce a low number of large, high quality offspring (Wheeler et al., 2020). These life-history traits make them particularly vulnerable to changes in their breeding migration patterns, which could lead to lower breeding success. Given that sharks, as apex predators or mesopredators, are crucial to a healthy ecosystem, any reduction in their fitness could have ecosystem-wide consequences. Therefore, understanding these different migration patterns is important for effective management of sharks. This is particularly important considering that transboundary marine species have an increased risk of overexploitation as management strategies vary among exclusive economic zones (Barkley et al., 2019).

The Port Jackson shark, *Heterodontus portusjacksoni*, is an endemic benthic Australian species (O'Gower, 1995). It is a good model species to study migration patterns as individuals display high levels of philopatry to their breeding grounds with 83% returning to Jervis Bay over multiple seasons (Bass et al., 2017). Previous studies on these sharks and their breeding migrations in Jervis Bay provide a strong basis for research on their movements at this study site (Bass et al., 2017, 2021, 2023; Day et al., 2019; Kadar et al., 2019). However, these studies have not investigated the potential environmental drivers of these migrations. Further research on the importance of environmental cues on the migration phenology of benthic sharks is required to increase our understanding of their ecology and vulnerability to climate change. As adults, Port Jackson sharks migrate up to 800 km between their feeding and breeding grounds and can reach depths of 275 m (Bass et al., 2017; Schieber et al., 2012). They travel from the unpredictable Bass Strait where they spend the summer foraging to the calm waters of Jervis Bay to breed, laying their eggs (maximum 16 eggs per annum) in the crevices of shallow, rocky reefs (McLaughlin & O'Gower, 1971; Powter & Gladstone, 2008b). This adaptability allows Port Jackson sharks to thrive in a wide range of environments, with varying oceanographic parameters.

We investigated the annual migratory patterns of Port Jackson sharks at a breeding aggregation site in Jervis Bay over a 7-year period using acoustic detection data. We addressed two key questions: (1) Are there temporal patterns in the migration timing among and within individual Port Jackson sharks to their breeding ground? (2) Do environmental (moon phase, period of day, rainfall, East Australian current (EAC) strength and sea surface temperature anomaly (sst)) and/or biological factors (sex and size) influence migration timing? We hypothesized that both environmental and biological factors influenced the migration timing of these sharks. For example, sharks are likely to reach the bay when sst promotes egg development, as higher temperatures ($+3$ °C) significantly increase mortality rates of juveniles (Vila Pouca et al., 2019). This is especially relevant, as the east coast of Australia has one of the highest rates of increase in ocean temperature due to anthropogenic climate change (Varela et al., 2018). Sharks using olfaction may also avoid heavy rainfall, which can mask the chemical smell of predators and increases nutrient loads in the bay where they breed (Leduc et al., 2009). We also hypothesized that males would arrive and leave earlier than females and that migration timing may differ by size (Bass et al., 2017). Additionally, we expected sharks to take advantage of EAC velocities to save energy during their migration. A previous study revealed that the timing of Port Jackson sharks' southward and northward movements matched the maximum and minimum velocities of the EAC (O'Gower & Nash, 1978), and migration speed was faster when travelling south with the current than when travelling north against it (Bass et al., 2017). As nocturnal sharks, we also expected them to migrate during the night. Finally, sharks might use the moon phase to optimize their migration and energy expenditure

with tides (Andrzejaczek et al., 2025; Dewar et al., 2008). Together, these hypotheses imply that arrival and departure dates should vary between years at the individual and population levels. If this is the case, it may have important consequences for individual fitness and breeding success of these sharks, with potential ecosystem-wide implications (Gervais et al., 2021).

METHODS

Study Site

The migratory patterns of Port Jackson sharks were studied in Jervis Bay (35° 03′ 20.40″ S, 150° 44′ 10.19″ E), a 102 km² oceanic embayment on the southern coast of New South Wales, Australia (Fig. 1). This bay is fed by multiple creeks and is an important breeding aggregation site for Port Jackson sharks (O'Gower, 1995). Thirty-six acoustic receivers (VR2W 69 kHz; Vemco, Halifax, Canada) were deployed in the bay, with eight receivers installed as gates at the bay's mouth to detect shark arrivals and departures (Fig. 1). The receiver detection range was 250 m (50% detection probability; Swadling et al., 2020). There was negligible variation between day and night (Bass et al., 2017).

Tagging

The migration timing of sharks was examined using passive acoustic telemetry, an effective method for monitoring the long-term movements of mobile marine species (Harcourt et al., 2019). Port Jackson sharks were considered to be sexually mature based on their size (males ≥ 750 mm LT; females ≥ 900 mm LT) and were tagged during the 2012−2014 breeding seasons (Powter & Gladstone, 2008b; Powter et al., 2010). The sharks were
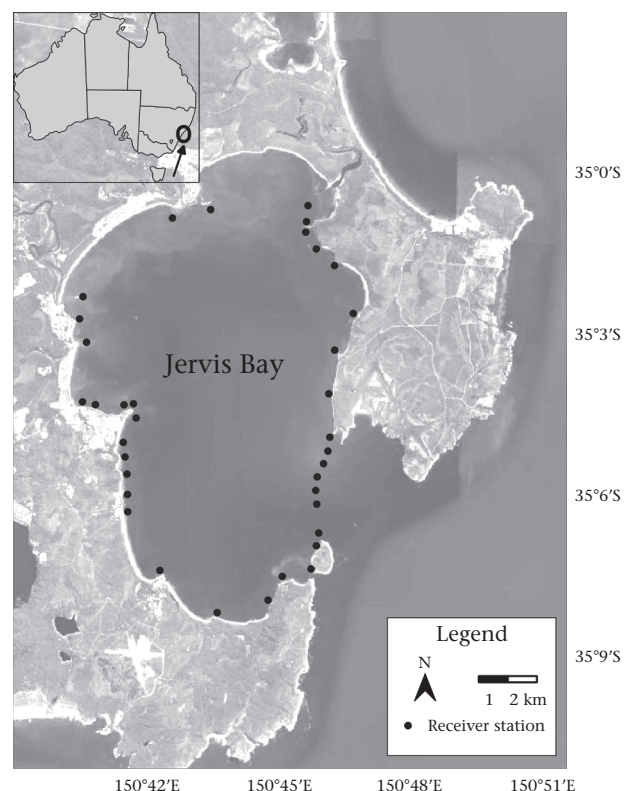

Figure 1. Map of the study area with the location of the acoustic receivers used during the study period (2013−2019).

hand captured by SCUBA divers and snorkellers and slowly brought to the surface (Bass et al., 2017). Sharks were then transported to shore (<30 m away) in a fresh seawater container (1.5 m × 0.4 m × 0.25 m) in a canoe. Transport took <5 min. Briefly, sharks were measured and sexed based on the presence or absence of claspers. Individuals were sedated in a solution of tricaine methanesulphonate (MS-222; 150 mg/mL) and an acoustic transmitter (V16-x 69 kHz transmitter; length: 6.8 cm, weight in water: 10 g; Vemco) was implanted in their peritoneal cavity through a 2.5 cm incision, which was then sutured using five interrupted sutures and superglue (Bass et al., 2017). Recovery from the anaesthetic took less than 5 min, then sharks were released where they were captured. The size of the transmitter was small relative to the sharks. On average, the sharks weighed 16 kg and measured approximately 1 m for a tag of 6.8 cm. The tags were programmed for 90−180 s intervals, with a battery life of 7.5−10 years. Resident individuals ($N = 3$), those with identical arrival and departure dates ($N = 2$) and those with unknown sex ($N = 2$) were excluded, leaving 47 sharks (25 males, 22 females) over seven breeding seasons (2013−2019; Fig. 2). Then, only individuals that came back more than 1 year to Jervis Bay were included for analyses to improve model fit (N between 43 and 45).

Acoustic Detection Data

Detection data were extracted from the Integrated Marine Observing System (IMOS) animal tracking database. In Jervis Bay, an individual was only considered to be present at any receiver if two or more detections of that individual were recorded over a 24 h period (Fig. 2). This screening procedure was used to control spurious detection or tag collisions (Bass et al., 2021). The date and time (day versus night) of arrival and departure of each shark in a given year were estimated as the first and last detection records for that shark at the breeding ground. This approach helped us define the migratory patterns of Port Jackson sharks, as most sharks breeding in Jervis Bay do not usually visit other neighbouring bays to breed and then leave for their foraging grounds (unpublished data). The number of individuals included in the analyses increased from 13−49 over the 7-year period as more sharks were tagged. Detections obtained during the first year when an individual was tagged were excluded from the analyses, as tagging occurred in the middle of the breeding season. The arrival and departure dates for a given year were expressed as the number of days since 1 January for that year (hereafter referred to as the Julian date).
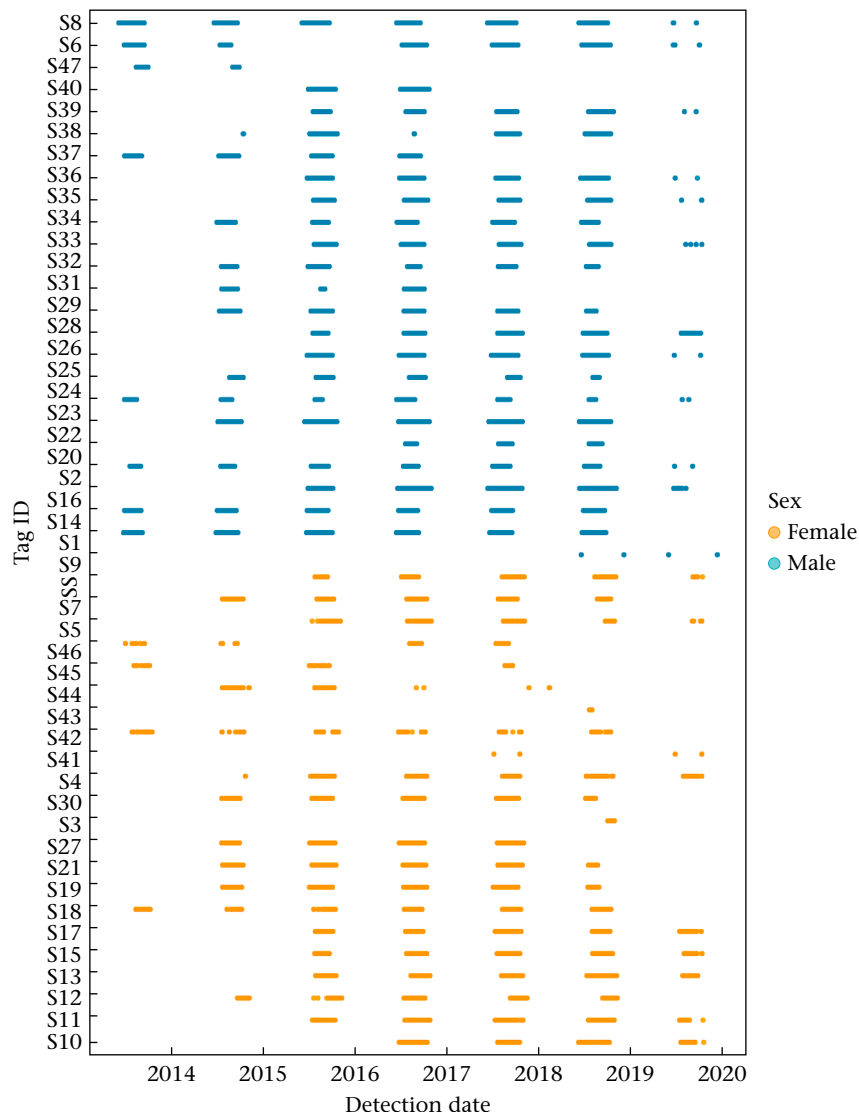
Figure 2. Acoustic detections (females: orange, males: blue) across all receivers for the 47 tagged sharks over the study period (2013−2019).

Environmental Predictors

The environmental variables (Table S1) were extracted for dates from 1 June−11 December (the earliest arrival date and latest departure date in the dataset). Daily rainfall data (mm) were extracted from the Australian Bureau of Meteorology database from the closest weather station: Point Perpendicular (AWS Station 068151, Jervis Bay, NSW). The daily sea surface temperature anomaly (°C) was calculated from the remotely sensed skin sea surface temperature (sst) at a depth of ~10 m. The initial data was obtained from the IMOS via the Australian Ocean Data Network online portal. Missing data owing to cloud coverage interfering with the satellite was filled in using the average of the day preceding and/or following the missing date. The completed daily temperature data of the last 31 years was then used to calculate daily sst anomalies. These sst means were used as a reference from which the daily sst means for the study years (2013−2019) were subtracted to calculate the temperature anomaly for the day of that year (anomaly $_{\text{day X, year X}}$ = sst.mean$_{\text{day X, year X}}$ − sst.reference. mean$_{\text{day X}}$). The daily strength of the EAC (Sv) was estimated using EAC southward transport ($Sv = 10^6$ m^3/s) from the mooring array off Brisbane, Australia (2012−2022; Sloyan et al., 2024). Transport was calculated as the sum of the current velocity times in the upper water column (0−1500 m) across the mooring array using the gridded data available from the CSIRO data portal. Between August 2013 and May 2015, the mooring array was not in the water, so there are no EAC transport estimates for this period. Moon phase, a proxy for illumination and tides, was extracted using the 'suncalc' package and the 'getMoonIllumination' function in RStudio (Thieurmel et al., 2022). The variables were then converted into categorical variables with four levels for analysis: first quarter (0.125−0.375), full moon (0.375−0.625), last quarter (0.625−0.875) and new moon (>0.875 or <0.125). The period of the day was also extracted with the 'suncalc' package and the 'getSunlightTimes' function, which uses the sunrise and sunset times of the arrival and departure dates of the sharks.

Data Analysis

Linear mixed-effects models were fitted to investigate the variations within and among individual sharks in the timing and consistency of their Julian arrival and departure dates over multiple years. The Julian date was treated as the response, and the shark ID and year were treated as random effects on the intercept. The models were fitted using the 'lme()' function in the R package 'nlme' to model heterogeneous variance with the 'VarPower' function, which was evident in our arrival data. The candidate predictor variables included: sex (levels: M, F), mean centred total length (quantitative; range: Female 109.5−131.0 cm, Male: 87.5−112.7 cm), rainfall (numerical), sst anomaly (numerical) and EAC (numerical). Models with all possible subsets of these predictors were fitted using the 'dredge' function in the R package 'MuMIn'. Informative predictors were selected from among the candidates by comparing the models using the Akaike information criterion corrected for small sample sizes (AICc). The variables selected in the best-ranked models were tested for interaction. The significance of fixed effects in lme models judged to be of the highest rank because AICc was assessed using likelihood ratio tests. EAC strength was investigated in preliminary analyses; however, statistics involving EAC were excluded from the results for two reasons. First, there were missing values for EAC (August 2013−May 2015), so analyses and model comparisons could only be run on a subset of the data. Second, for the arrival, the EAC variable was never included in the models within two AIC units of

the best models and was included for departure but was not significant (see Table S2−S4).

Repeatability coefficients (R) were calculated with the default settings of the 'rptR' package for the best Julian arrival and departure models. The repeatability of the Julian arrival was calculated using a subset of the data, excluding two arrivals after day 230, which were largely responsible for the observed heterogeneous variance (Stoffel et al., 2017). For comparison, the repeatability on the full dataset for Julian arrival, including error variance, and was very similar (see Table S5).

Separate models were used to disentangle the influence of tides represented by the moon phase with the illumination of the period of the day on the migration patterns. We fitted generalized linear models with Poisson distributions to investigate whether more sharks arrived or departed from their breeding grounds during the day or during a particular moon phase. The response variable was the number of sharks tallied each year with respect to each of the eight combinations of levels for two categorical predictor variables: moon phase (four levels) and period of the day (two levels). An offset term with the logarithm of the number of sharks tallied across all combinations of levels in a given year was included to adjust for the varying sample sizes. Overdispersion and interactions were not found to be significant. Year was not included as a random effect as it was redundant with the offset term and did not account for any deviance.

All statistical analyses were performed using RStudio 4.1.3. The main packages used in RStudio were: 'tidyverse' (Wickham et al., 2019), 'lme4' (Bates et al., 2015) and 'mgcv' (Wood, 2017). We report P values for coefficient fitted models but note that cautious interpretation is warranted, given that type I error rates exceed the nominal reported values whenever multiple competing models are fitted and compared.

Ethical Note

All capture and tagging procedures were conducted in accordance with an Animal Research Authority permit (2012/009) granted by the Macquarie University Animal Ethics Committee and two NSW Fisheries permits (P08/0010−3.1 and P08/0010−4.2). Sharks were gently handled during capture while scuba diving or snorkelling. These capture methods were preferred over fishing gear to minimize stress for the sharks. They were brought to the surface very slowly to prevent any injuries. Once at the surface, sharks were anaesthetized to reduce pain during tag insertion. The smallest acoustic tags were selected to minimize incision size and time under anaesthesia for the shark. Minimum handling time was used to conduct the surgery (<5 min) and allow recovery. An anaesthetic was administered during the procedure. Sharks were only released when they were strong enough to break free, which indicated good recovery from the surgery. The year the sharks were tagged was excluded from analyses as tagging occurred in the middle of the breeding season. This helped to account for any potential behavioural impact from the procedure. After their release, all sharks came back to their breeding grounds in the following years, indicating there was no mortality.

RESULTS

Arrival

The arrival dates of Port Jackson sharks ($N = 47$) varied by more than 4 months for the 47 sharks included in our analysis during the study period 2013−2019, with the earliest being 1 June (Julian day 152) and the latest being 14 October (Julian day 287; Fig. 3a). The average arrival dates varied by only 14 days among years, from 12

July (mean ± SE for Julian day: 193 ± 3 days) in 2016 to 26 July (207 ± 5 days) in 2014 (Table S6). The average Julian arrival date varied substantially among sharks, from a minimum of 10 June (mean ± SE for Julian day: 161 ± 9 days) to a maximum of 2 October (mean Julian day: 275, single observation; Fig. 3a–Table S7). Moreover, sharks with later average arrival dates also showed greater variation in arrival date from year to year (Fig. 3a). To address this issue of heterogeneous variance, we assumed that the residual variance increased as a power function of the fitted value when selecting informative predictors from among candidates for arrival dates.

After accounting for random effects on the intercept attributable to year and shark ID ($N = 43$), sst anomaly, rainfall and sex met our criteria for inclusion in the final arrival-date model, meaning that they were incorporated as predictors into models within two AICc units of the model with the lowest score (Table S8). Likelihood ratio tests indicated that sex had far greater predictive power (chi-square test: $\chi^2_1 = 13.33$, $P < 0.001$) than rainfall (chi-square test: $\chi^2_1 = 1.09$, $P = 0.30$) and sst anomaly (chi-square test: $\chi^2_1 = 0.45$, $P = 0.50$) in this final model (Table S9). On average, males arrived on 8 July (mean ± SE for Julian day: 189 ± 2 days), and females arrived ~18 days later on 26 July (mean ± SE for Julian day: 207 ± 2 days; Fig. 4a). There was no significant interaction between sex and sst anomaly and rainfall. Our decision to treat error variances as heterogeneous using a power function is supported by an AIC comparison of this final model with a simplified version that incorporates the same fixed- and random-effect predictors but assumes constant error variance (AIC is 40 units lower).

Using this simplified version to facilitate approximate partitioning of variance among variables (Table S5), we found that shark ID ($N = 43$) accounted for by far the largest fraction of the variance ($r = 42\%$), followed by sex ($r^2_m = 17\%$), year ($r = 5\%$), rainfall ($r^2_m = 0.09\%$) and sst anomaly ($r^2_m = 0.04\%$). The calculated repeatability for shark ID in this model was 51% ($r = 0.51$, CI = [0.35, 0.64]), indicating pronounced differences among sharks in

their typical arrival dates, even after accounting for sex, which was consistent across years.

To assess whether arrivals varied with time of day, we fit a separate model that incorporated the moon phase and period of the day as fixed effects and an offset term with the logarithm of the number of sharks ($N = 45$) tallied across all combinations of levels in a given year to adjust for the varying sample sizes. The results of this analysis indicated that the period of the day significantly explained the variation observed in the counts of arrivals (LR chi-square test: $\chi^2_1 = 90.24$, $P < 0.001$), with 174 arrivals during the night compared with 37 during the day (Table S10). Approximately 83% of sharks arrived during the night across all years. There was no significant sex difference in arrivals during moon phases or period of the day.
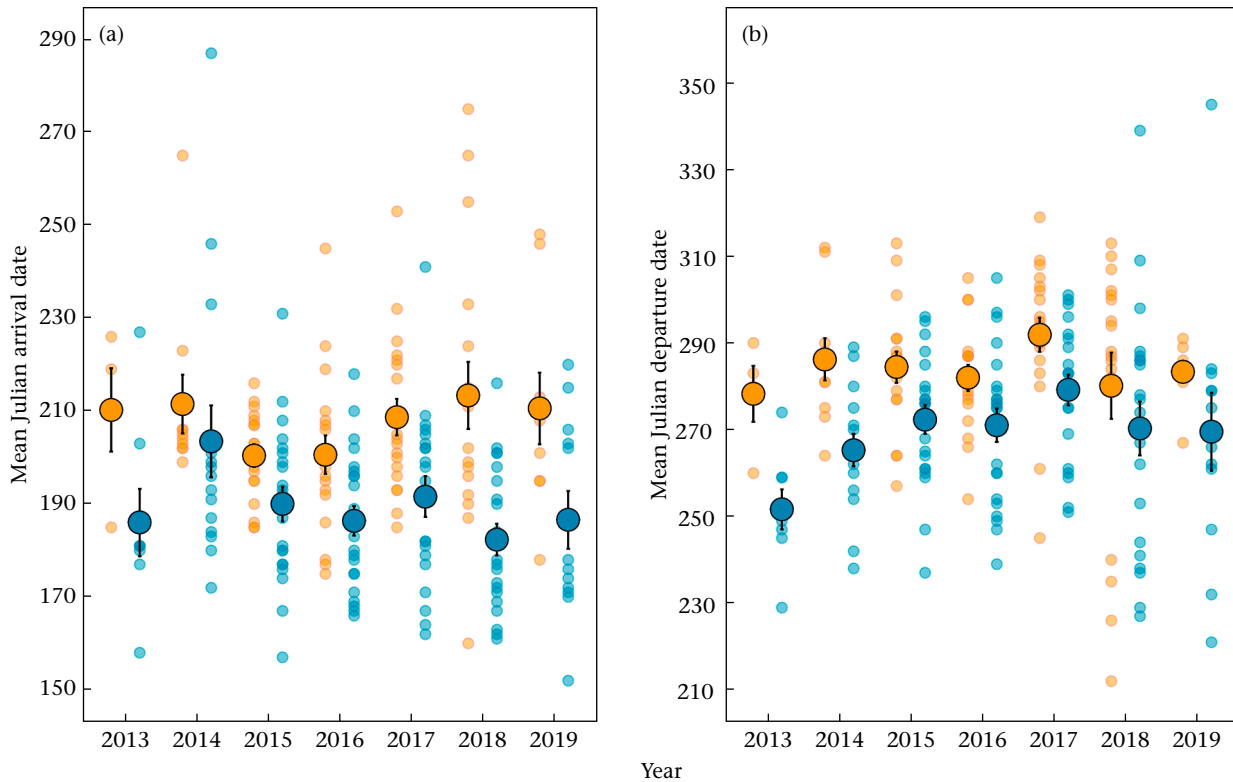
Departure

The departure dates of Port Jackson sharks ($N = 47$) varied by >4.5 months over the study period; the earliest being 31 July (Julian day 212), and the latest being 11 December (Julian day 345; Fig. 3b). The average departure dates varied by 24 days among years, from 18 September (mean ± SE for Julian day: 261 ± 5 days) in 2013 to 12 October (mean ± SE for Julian day: 285 ± 3 days) in 2017 (Table S6). The average Julian departure date varied substantially among sharks, from a minimum of 31 July (mean ± SE for Julian day: 212, single observation) to a maximum of 8 December (mean ± SE for Julian day: 342 ± 3 days; Fig. 3b–Table S7). Furthermore, sharks with departure dates in the middle of the breeding season also presented greater variation (SD) in their departure dates from year to year (Fig. 3b).

After accounting for random effects on the intercept attributable to year and shark ID, sex and rainfall met our criteria for inclusion in the final departure-date model, meaning that only these variables were incorporated as predictors into models within two
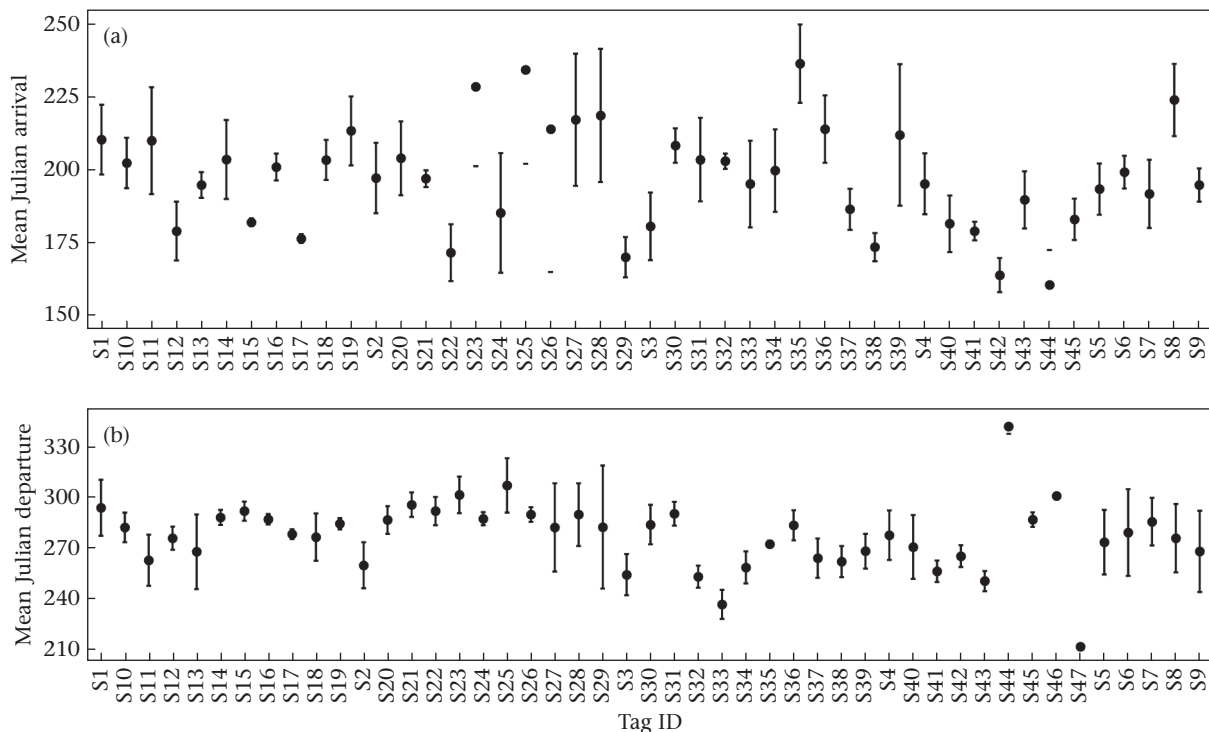
Figure 3. (a) Mean Julian arrival date and (b) departure date for each shark ($N = 47$) over the study period (2013–2019). Whisker length corresponds to SD of the mean. Individuals are sorted by Tag ID.

Figure 4. (a) Mean Julian arrival date per sex (females: orange, males: blue) per year to Jervis Bay ($N = 47$). (b) Mean Julian departure date per sex per year to Jervis Bay. The error bars represent the SE.

AICc units of the model with the lowest score (Table S11). Likelihood ratio tests indicated that rainfall (chi-square test: $\chi^2_1 = 0.54$, $P = 0.46$) was not significant (Table S12). However, sex (chi-square test: $\chi^2_1 = 10.87$, $P < 0.001$) was significant. On average, males departed on 27 September (mean $\pm$ SE for Julian day: 270 ± 2 days) and females departed on 11 October (mean $\pm$ SE for Julian day: 284 ± 2 days; Fig. 4b). There was no significant interaction between sex and rainfall.

Using approximate partitioning of variance among variables (Table S13), we found that shark ID ($N = 43$) accounted for by far the largest fraction of the variance ($r = 35\%$), followed by sex ($r^2_m = 12\%$). year ($r = 7\%$) and rainfall ($r^2_m = 0.2\%$). The calculated repeatability for shark ID in this model was 40% ($r = 0.40$, CI = [0.22, 0.55]), indicating pronounced differences among sharks in their typical departure dates, which were consistent across years.

To assess whether departures varied with time of day or moon phase, we fit a separate model that incorporated the moon phase and period of the day as fixed effects and an offset term with the logarithm of the number of sharks tallied ($N = 45$) across all combinations of levels in a given year to adjust for the varying sample sizes. The results of this analysis indicate that the period of day significantly explained the variation observed in the counts of departures (LR chi-square test: $\chi^2_1 = 22.48$, $P < 0.001$), with 145 departures made during the night compared with 66 during the day (Table S14). Approximately 70% of sharks departed during the night across all years.

Additionally, strong site fidelity was observed, with high individual return rates to the breeding ground every year. On average, 75% of the females and 80% of the males returned to Jervis Bay over the 7-year period (Table S15 and S16).

DISCUSSION

This study presents long-term acoustic monitoring of the migration patterns of Port Jackson sharks at a breeding aggregation site in Jervis Bay. While previous studies have mainly explored the influence of sst on migration timing, they have not addressed the influence of other environmental parameters on longer term individual tracking data for benthic sharks. We found that, on average, shark arrivals and departures were relatively consistent. This variation was explained mostly by individual ID and somewhat by year and sex. However, a third of the variance in the arrival and departure of sharks remains unexplained and warrants further investigation. Additionally, in this study, more sharks tended to arrive and depart from their breeding ground at night, consistent with their nocturnal nature.

We found temporal patterns in migration timing among and within individual Port Jackson sharks. The proportions of total variance in arrival and departure dates explained by year were 5% and 7%, respectively. This was translated by annual variability in the arrival and departure dates among sharks and the 7-year study period (2013–2019). A similar pattern was observed in white sharks, *Carcharodon carcharias*, which display annual variability in movements (mean = 66.8 $\pm$ 21.6 days) across sharks and years (2017–2020; Franks et al., 2021). We also found pronounced differences among individual sharks in their arrival ($r = 0.51$) and departure ($r = 0.40$) that were consistent across years. These repeatability coefficients align with other studies on animal migration timing, which typically ranged from $r = 0.20$ to $r = 0.72$ (Bêty et al., 2004; Fraser et al., 2019; Kürten et al., 2022; Oosthuizen et al., 2023). These data strongly suggest that migration timing is a stable individual trait.

We also found that variance in migration timing was also partly explained by sex (arrival: 17%, departure: 12%). Males initiated their migration 2 weeks earlier than females, which is consistent with previous studies (Bass et al., 2017; Pillans et al., 2021). Similarly, males, on average, also departed 2 weeks earlier than females. Male Lemon sharks, *Negaprion acutidens*, depart 1 to 2 months earlier than females, and male nurse sharks, *Ginglymostoma cirratum*, also arrive earlier at their breeding ground than females (Pillans et al., 2021; Pratt et al., 2022). These patterns could be due to different sexual environmental preferences, owing to contrasting life-history priorities. Port Jackson shark females might also arrive at Jervis Bay later than males, as they require a greater food supply at their foraging grounds to compensate for greater energy expenditure during breeding and their larger sizes (Weng et al., 2008). Males may also arrive early at setting up territories and intercepting females as they arrive (Bass et al., 2021). Bisexual philopatry is rare in shark species and has important implications for their population structure (Day et al., 2019). Subpopulations can limit the genetic diversity of individuals within the population and may lead to inbreeding. However, long-term site fidelity, as observed in this study, may increase individual fitness through spatial familiarity or local adaptation (Gervais et al., 2021; Knip et al., 2012).

This study revealed that most Port Jackson sharks arrived and departed from Jervis Bay during the night. Many species of elasmobranchs, including Port Jackson sharks, are nocturnal and show relatively high activity levels at night (Nelson & Johnson, 1970), which explains why they are more likely to leave and arrive from the breeding grounds during the night. A study on Port Jackson sharks revealed that although most tagged individuals were nocturnal, a small number of sharks were detected more frequently during the day, possibly to reduce competition for resources (Bass et al., 2021). We also found a small proportion of sharks arrived and departed during the day; these activity patterns could be due to phenotypic plasticity (Kadar et al., 2019). Although the moon phase did not influence arrivals or departures, as it was used as a proxy for both tides and illumination, it remains challenging to disentangle their individual ecological contributions. Most of the variance in migration timing was explained by individual ID, but a third was unexplained by any of our predictors. Port Jackson sharks may use different cues (e.g. social cues) to initiate migration. For example, blue whales, *Balaenoptera musculus*, can use social cues to learn their migration routes/timing rather than relying on environmental cues (Dodson et al., 2024). Perhaps juvenile Port Jackson sharks follow adults once they leave breeding and nursery grounds for the first time. Social influences (social learning and culture) can positively impact the accuracy of the individual migration of several species through different mechanisms (Aikens et al., 2022; Oestreich et al., 2022). Social learning of migratory behaviour can enhance the ability of naïve individuals to track environmental variability through space and time and increase the efficiency of migration across generations (swarm intelligence; Berdahl et al., 2018; Couzin, 2007). Social network analyses have indicated that Port Jackson sharks live in structured societies and that social relationships during the breeding season can predict their arrival and departure dates (Mourier et al., 2017; Vila Pouca et al., 2020). However, high fidelity to cultural traditions can also be maladaptive if there is a mismatch between cultural behaviour and contemporary conditions (Aplin, 2019; Laland & Williams, 1998). Further research on the influence of the heritability of migration timing and the importance of cultural transmission on the migration of sharks is needed (Helm et al., 2006).

The remaining variance in migration timing could also be explained by local environmental variables at the foraging grounds from which the Port Jackson sharks depart. The movements of benthic marine animals are particularly challenging to study on such broad scales. Some of these sharks are migrating >1000 km. For acoustic telemetry, benthic sharks are harder to study compared with more mobile coastal species because they live close to the seafloor, where the environment can interfere with acoustic signals (Mourier et al., 2017). The location of the Port Jackson shark's foraging grounds has not been identified, but the Jervis Bay sharks are detected down the east coast of Australia all the way to King Island and Bass Strait. Therefore, investigating environmental variables at the foraging grounds would be particularly challenging using acoustic telemetry. Setting up and maintaining acoustic stations in these remote areas is extremely expensive. For satellite telemetry, sharks usually need to surface to transmit data, except for pop-off archival tags, as they detach from the shark on their own to transmit the data to the satellite (Matley et al., 2022). Future studies could benefit from the use of pop-off archival tags on small migratory benthic shark species to gather data on the entirety of their migratory route. However, these tags are very expensive, making it difficult to obtain good sample sizes.

Surprisingly, sst at the breeding grounds of Port Jackson sharks did not influence their migration timing. It is possible that this flexibility helps them to maintain their breeding synchrony over time. However, sst is rapidly increasing on the east coast of Australia due to climate change and may become incompatible with juvenile survival. Port Jackson shark eggs incubated and reared at projected end-of-century temperatures ($+3 \,°C$) presented mortality rates 41.7% higher than those reared at present-day temperatures (Vila Pouca et al., 2019). Higher temperatures can alter growth, muscle metabolic features, brain morphology, sensory systems and cognition, increasing the vulnerability of this species to climate change (Izzo & Gillanders, 2020; Peele et al., 2023; Thomas et al., 2023). Additionally, these sharks have a long mean generation time ($\mu_1 = 22.5$ years) making them even more susceptible to population declines that could take years to become apparent (Powter & Gladstone, 2008a). Therefore, it is likely that juvenile Port Jackson sharks will experience lower survival if their parents do not track sst to time their migration and lay their eggs in favourable environments. More research comparing resident sharks and the environmental factors that they experience all year round in the bay to the migratory sharks would provide a greater understanding of their plasticity. This could lead to serious detrimental consequences for populations and ecosystems of these mesopredators. Future studies could use pop-off archival tags to (1) determine what sst conditions these sharks experience at both breeding and foraging grounds to analyse whether there is any influence of sst on migration timing and (2) quantify the juvenile survival rate of these individuals based on the sst in Jervis Bay.

This study found no influence of sst and EAC strength on the migration timing of Port Jackson sharks. The absence of a detectable effect could be due to a mismatch between predictor completeness and shark behaviour. Missing data is a common issue in environmental variables and was evident for both EAC strength and sst. The sst data in this study was extracted from a single-sensor multisatellite. This sensor was chosen as it had the most data for our study area and study period compared with other sensors available on IMOS. This sensor used high-quality data from the advanced high-resolution radiometer on all available National Oceanic and Atmospheric Administration polar-orbiting satellites. However, there were still data gaps that were filled using averages. Similarly, the EAC strength data was also of high quality, but data was missing between August 2013 and May 2015 due to the mooring array being out of the water. Studying parameters including salinity, sea surface height and geostrophic

flow would help future studies investigate the influence of environmental cues on the migration timing of these sharks.

In summary, Port Jackson sharks showed annual variability in their breeding migration timing independent of variation in the environmental conditions at their breeding grounds. Migration timing was explained mostly by individual variation, sex and year. We also found that more sharks arrived and departed from Jervis Bay during the night. These sharks are capable of incredible phenotypic flexibility to adapt to different environments and maintain their breeding synchrony (Bass Strait versus Jervis Bay). However, these consistent migration patterns are concerning for the survival of juvenile Port Jackson sharks, which have relatively high mortality rates at higher sst. Further research should focus on investigating the role of different cues, including social cues, on the migration timing of these sharks. Additionally, using satellite telemetry with pop-off archival tags could help future studies to gather sst data at both breeding and foraging grounds to help us understand the link between the temperature and movements of these benthic sharks. This could help us quantify the potential detrimental impact it could have on juveniles, leaving important populations for ecosystem consequences for these mesopredators.

Author Contributions

Loéva Martin-Podevin: Writing − review & editing, Writing − original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Juliette Tariel-Adam:** Writing − review & editing, Visualization, Validation, Methodology, Formal analysis. **Andrew P. Allen:** Writing − review & editing, Validation, Methodology, Formal analysis. **Nathan Bass:** Funding acquisition. **Tristan Guttridge:** Writing − review & editing, Funding acquisition. **Culum Brown:** Writing − review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Data Availability

Declaration of Interest

The authors declare that they have no affiliations with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123370.

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