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Ranging patterns and mortality of an at-risk marine mammal resident in a highly urbanized estuary

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Understanding the ranging patterns of wildlife populations can help identify potential factors contributing to stress, injury, reduced reproductive success, deteriorating health, mortality and displacement from or avoidance of biologically important areas. This study used photographic identification data collected over a 33-year period to characterize the ranging patterns of the Near Threatened Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, inhabiting the highly urbanized Port River estuary in South Australia. Using kernel density methods, we assessed if ranging patterns differed in size and location by sex and if they were associated with a recent increase in dolphin mortalities. Three locations within the study area were identified as core areas of use for multiple individual dolphins over the 33-year period. The ranging patterns of frequently sighted individual dolphins showed no significant differences in core and representative range size and location by sex, or whether a dolphin was deceased or still alive in the study area. In contrast, dolphins that recently died (2018–2022) had core areas of use concentrated in a single, restricted region of the study area. These core ranges were smaller than those of other individuals in the population, highlighting a potential spatiotemporal component to the recent increase in dolphin mortalities. Subsequent research on potential stressors associated with this dolphin core area of use should aid in the identification of contributing factors to the recent mortalities and assist conservation management decisions. This study highlights the significance of long-term monitoring and understanding wildlife ranging patterns in identifying potential human–wildlife conflicts.

The way animals use space and their patterns of movement are important to all organisms and play a major role in determining the fate of individuals (Brown & Orians, 1970; Morales et al., 2010). Thus, quantifying animal space use and movement patterns is important to understand their ecology and is an essential component of the effective management and conservation of species (Boyle, 2021; Lédée et al., 2015). Movement patterns, or ranging behaviour, are assumed to be an expression of the animals' responses to access spatially and temporally distributed resources (e.g. prey availability, shelter, mating opportunities), while avoiding predators, in a way that improves their fitness (Burt, 1943; Knüsel et al., 2019). The spatial extent of the area traversed by an animal in the process of acquiring food, mating and rearing offspring (i.e. their 'home range', Burt, 1943) depends on the type, abundance and composition of these resources across the available habitat; however, there is a trade-off between acquiring these resources and energy expenditure (Knüsel et al., 2019). Many animal species do not use space uniformly, with individuals differing in their spatial coverage and intensity of use within their ranging patterns (Rodriguez et al., 2021). Commonly used areas, also known as 'core areas of use' or 'core ranges', are used more frequently than the rest of the overall range (also called a 'home range' or 'representative range'), implying that the core range contains the most important and dependable resources, and thus represents an important ecological area (Gowans et al., 2008; Klevtcova et al., 2021).

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Animal ranging patterns may be restricted by naturally occurring physical barriers (e.g. mountains, rivers or coastlines, Knight et al., 2009; Zenzal et al., 2018), confined by fragmented habitats (Boyle et al., 2009) or modified by anthropogenic activities such as urban development (Watson-Capps & Mann, 2005). For marine mammals, urban development and industrialization of coastal environments have the potential to affect their ranging patterns through noise and water pollution and overall changes to habitat quality (Pirotta et al., 2013; Rako et al., 2013; Watson-Capps & Mann, 2005). This can lead to animal displacement, smaller home ranges, fragmentation of populations and reduced gene flow, as well as loss of species diversity (Sol et al., 2013; Teitelbaum et al., 2020). Small delphinid populations occupying restricted ranges are particularly vulnerable to population decline due to localized threats and increased exposure to natural or anthropogenic pressures (Passadore et al., 2018; Reisinger et al., 2022). For example, the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, is classed as a ‘Near Threatened’ species (IUCN, 2023) due to its relatively small, fragmented and restricted near-shore distribution, proximity to anthropogenic threats, vulnerability to entanglements and population declines in several areas (Braulik et al., 2019). Increasing rates of urbanization and human use of coastal areas may expose these dolphins to cumulative natural stressors (e.g. harmful algal blooms, diseases, freshwater inflows, terrestrial runoff) and anthropogenic pressures (e.g. noise and chemical pollution, dredging and construction, fishing and shipping), the effects of which are amplified due to the dolphins' generally year-round residency and relatively small individual home ranges (Kirkwood et al., 2022; Passadore et al., 2018; Phillips & Rosel, 2014; Sprogis et al., 2016; Wang, 2018). Understanding what areas animals use and where these areas are located can inform strategies for managing populations and mitigating effects from anthropogenic pressures (e.g. urban development, pollution) and human–wildlife conflicts (e.g. interactions with fisheries, disturbance from vessel movements; Boyle, 2021).

Estimating delphinid home and core ranges can be complex due to the many intrinsic and extrinsic factors affecting their movements, including age class (McHugh et al., 2011; Tsai & Mann, 2013), sex (Fury et al., 2013; Passadore et al., 2017; Wells et al., 2017), mating opportunities (Sprogis et al., 2016), reproductive state (Gibson et al., 2013), prey distribution (Heithaus & Dill, 2002; McCluskey et al., 2016) and predator occurrence (Heithaus & Dill, 2002), along with environmental factors such as temperature and salinity (de Moura et al., 2021; Mintzer & Fazioli, 2021; Rodriguez et al., 2021), water depth (de Moura et al., 2021; Flores & Bazzalo, 2004; Fury et al., 2013; Passadore et al., 2018) and habitat characteristics (Passadore et al., 2017; Sprogis et al., 2016). The effects of these factors on delphinid ranging patterns can vary across species and populations. For example, delphinid males are generally expected to have larger ranges, related to seeking mating opportunities (e.g. Sprogis et al., 2016; Urian et al., 2009; Wells et al., 2017). However, studies have found alternative patterns, such as equivalent range sizes between sexes (Passadore et al., 2017) and females with larger ranges than males (Flores & Bazzalo, 2004; Fury et al., 2013). Home ranges may also vary in response to different social or environmental conditions due to the behavioural flexibility of the species (Boyle, 2021), requiring longitudinal data (i.e. systematically measuring the same individuals repeatedly over time; Mann & Karniski, 2017) to fully understand the drivers underpinning their home ranges.

Additional challenges arise when estimating movement patterns and home ranges for highly mobile marine species, such as dolphins, due to the technical difficulties of unobtrusively tracking these animals. Delphinids, and cetaceans in general, are fast moving and deep diving, spending most of their time out of view of researchers (Mann & Karniski, 2017). Animal-borne tags can provide detailed behavioural information of cetaceans occurring above and below the surface but are invasive and often expensive, mainly applied to larger species and generally only deployed for short periods of time (days to months) on a limited number of individuals (Mann & Karniski, 2017). Photographic identification (photo ID) of individual dolphins, using distinctive and naturally occurring markings on their dorsal fins that remain relatively stable through time, provides a noninvasive and relatively inexpensive alternative to collect individual-level data (Würsig & Jefferson, 1990; Würsig & Würsig, 1977). Delphinids are long lived (e.g. estimated maximum lifespan of *Tursiops* spp. is 40–50 years; Wang, 2018), making long-term monitoring (i.e. studies spanning over 5 years) important for capturing behavioural changes associated with age classes or environmental shifts. Most long-term cetacean studies have focused on coastal species due to their accessibility to researchers (Mann & Karniski, 2017); however, only a small subset of these studies have tracked individuals across multiple generations (e.g. Brent et al., 2015; Connor & Krützen, 2015; Wells, 2014). The most common approach to longitudinal monitoring of coastal cetaceans is through opportunistic or systematic surveys using photo ID techniques to record individual-level data (Mann & Karniski, 2017; Urian et al., 2015). Data sets produced by these long-term photo ID studies of cetaceans can provide the records necessary to ascertain variations of ranging patterns within a population.

A population of Indo-Pacific bottlenose dolphins, *T. aduncus*, inhabits the Port River estuary in South Australia. This population has been the subject of ongoing, long-term research since the late 1980s (Bossley et al., 2017). Based on systematic boat-based surveys and photo ID techniques, this research identified a total of 270 individuals in the Adelaide Dolphin Sanctuary from 1988 to 2020, with 102 classified as year-round resident animals (A. Steiner, personal communication., 29 September 2024). The number of dolphins sighted within the estuary varies over time, but the biological causes for this variability remain unclear (Bossley et al., 2017). Recent genetic analyses of deceased individual dolphins concluded that the dolphins inhabiting the Port River estuary are considered a genomically distinct population (Keep, 2022). The estuary has a long history of being heavily industrialized, with manufacturing wastes, heat and sewage effluents, as well as stormwater outflows, impacting the area since industrialization (Bossley et al., 2017; Lavery et al., 2009; Pfennig, 2008; Wade, 2002). Also, the ambient water quality was rated as poor to moderate in a 2000 environmental assessment report (Wade, 2002). Subsequent environmental improvement programs and policies have contributed to improved water quality in the Port River in recent decades. A reduction in water pollutant load was observed to coincide with a 6% annual increase in dolphin sightings in the inner estuary over a period of 24 years (1990–2013; Bossley et al., 2017). Although this population faces negligible predation pressure (Steiner & Bossley, 2008), previous anthropogenic threats to the survival of these dolphins have included deliberate attacks, boat strikes, entanglements and heavy metal absorption (Bossley et al., 2017; Byard et al., 2020; Lavery et al., 2008). The implementation of the Adelaide Dolphin Sanctuary (ADS) in 2005, mandated to protect both the dolphins and their habitats, has allayed some of these direct threats (Government of South Australia, 2005). Studies on dolphin deaths (*Tursiops* sp.) in the ADS between 1987 and 2013 showed an increase in mortality, with the estimated rate rising from 1.1 dolphins per year before the ADS (1987–2004) to 3.0 dolphins per year after the ADS was established (2005–2013; Adamczak et al., 2018; Kirkwood et al., 2022). The most recent report on *Tursiops* mortalities in the ADS, covering the period from 1987 to 2020, indicates a rise in mortalities since 2005. Estimated mortality rates increased to 2.8 dolphins per year from 2006 to

2010, then further to 4.6 dolphins per year from 2011 to 2015 and 4.2 dolphins per year from 2016 to 2022 (Tomo & Kemper, 2022a). Since 2018, eight dolphins exhibited acute changes in body condition (emaciation) prior to death or disappearing from the area (Department for Environment and Water, 2023; Tomo & Kemper, 2022a). Investigations into probable or likely causes of death in this dolphin population have thus far proved inconclusive (Kirkwood et al., 2022).

Understanding the spatial distribution of dolphins in the ADS and identifying their core and representative areas of use would help pinpoint risks they may face from human activities. This knowledge can guide further research into factors like water quality and prey health, which may interact with the dolphins' spatial distribution and lead to increased mortality rates. In this study, we used long-term (33 years) dolphin photo ID data collected throughout the southern section of the Adelaide Dolphin Sanctuary (study area) to: (1) estimate the size and spatial extent of individual dolphins' core areas of use and representative ranges, (2) assess differences between female and male dolphin ranging patterns and (3) determine whether there are any differences in the ranging patterns of recently deceased and alive individuals. Overall, this study advances our understanding of dolphins’ movement and space use in a highly urbanized environment and should contribute to informed conservation management decisions into the future.

METHODS

Study Area

The study area is located in the southern section of the Adelaide Dolphin Sanctuary (ADS), covering a 57 km^2 region, from the Port River/North Arm junction to approximately 6.5 km south of Port Gawler. The 118 km^2 ADS comprises a sheltered, marine-dominated inlet system located on the eastern side of Gulf St. Vincent in South Australia. The sanctuary boundary covers the Port Adelaide River, Outer Harbor, and follows the high-water mark along Barker Inlet northwards to Port Gawler, and approximately 3–5 km west out into the deeper gulf waters (Fig. 1a). The area is comprised of widespread seagrass meadows and mangrove forests, which serve as important nursery areas for juvenile fishes, along with intertidal mudflats and deeper dredged shipping channels (Bloomfield & Gillanders, 2005; Bossley et al., 2017; Henkens et al., 2022). This ecosystem experiences continuous tidal flushing with water from the gulf and low intermittent inflows of freshwater from creeks and stormwater runoff resulting in seasonally variable salinity between 35 and 41 psu (Jones et al., 1996; Kämpf, 2014). The surrounding land is of primarily industrial use to the east and southeast, and residential to the south and west. The Port River has a history of industrial and commercial manufacturing operations and is the main shipping port for South Australia. Past amelioration of anthropogenic pollutants (e.g. nitrogen and phosphorous from wastewater treatment and manufacturing industry outflows) has reduced many point sources of pollution in the area and yielded better water quality and a more promising environment; however, some pollutant constituents have probably accumulated in the benthos and food chain (Bossley et al., 2017; Kirkwood et al., 2022; Pfennig, 2008).

Data Collection

This study used data collected during boat-based surveys in the southern ADS along a predetermined route (see Fig. 1a) using powerboats ranging in size from 4 to 6 m in length, and in weather conditions with Beaufort Sea State <3 (for full survey methodology, see Bossley et al., 2017). The survey route covered the southern and central sections of the ADS, including shallow areas (e.g. Barker Inlet), deeper dredged shipping channels (e.g. Port River, Outer Harbor) and open waters of Gulf St. Vincent. Each survey was approximately 40 km in length and around 4 h in duration, with a maximum of one survey per day conducted. The circular route was designed to minimize the resighting of individual dolphins within a survey. Surveys that fully or partly covered the survey route were included in the analysis.

During most surveys, the location (latitude and longitude) of the dolphin groups sighted was recorded using a Global Positioning System (GPS), and dolphins were photographed for individual identification using the unique nicks and marks on their dorsal fins (Würsig & Jefferson, 1990), enabling sighting locations to be attributed to all identified individual dolphins within a group. Prior to May 1997, the location of each group sighting was mapped using triangulation methods with identifiable landmarks and shoreline features that were later converted to latitude and longitude coordinates.

Data filtering

The survey database contained 25 667 sighting records across 33 years (1988–2020) and 246 uniquely identified dolphins. Sighting locations with GPS coordinates suggestive of error (i.e. situated on land or well outside the survey area, $N = 1666$) were removed from analysis. Sighting records of unidentifiable individual dolphins (i.e. dolphins with no distinctive marks on their dorsal fins) were then excluded ($N = 9923$). Any resighting of a uniquely identifiable dolphin within the same survey (i.e. same day) was excluded to avoid spatial and temporal autocorrelation ($N = 492$). Finally, individual dolphins for which age class could not be determined ($N = 24$) were excluded from analysis.

Dolphin age and vital status

Dolphin age was estimated using a set of criteria based on physical size, presence of a female dolphin's first known calf, or observation as a neonate/calf (Steiner & Bossley, 2008). Ten years was set as a conservative age for maturity in both sexes (Kemper et al., 2014, 2019; Tsai & Mann, 2013) and for females (not observed from birth) when sighted with their first calf. Age classes were defined as: calf/juvenile (birth to 3 years), subadult (4–9 years) and adult (≥10 years; Kirkwood et al., 2022; Steiner & Bossley, 2008).

Dolphins were considered deceased if: (1) the body of the dead dolphin was retrieved and the individual identified (confirmed deceased); (2) the dolphin was not sighted for more than 2 years (presumed deceased); or (3) the dolphin was sighted with signs of severe ill health (e.g. emaciation, multiple/severe lacerations) prior to disappearance (presumed deceased). To incorporate the most recent dolphin mortalities in the analyses, the vital status of each dolphin (currently alive, confirmed deceased or presumed deceased) was recorded as of the end of 2022, as were the ages of dolphins still alive in the study area.

To further investigate the ranging patterns of deceased dolphins, we used necropsy reports (Department for Environment and Water, 2023; South Australian Museum, n.d.) to gather information on the circumstances of death and body condition, where available. These reports categorized the circumstances of death (e.g. disease, intentional killing, known entanglement) according to evidence gathered at the time of observation in the field, at necropsy and from pathology investigations carried out post necropsy (Tomo & Kemper, 2022b). For presumed deceased individuals, body condition prior to their disappearance was assessed through field observations and photographic records.

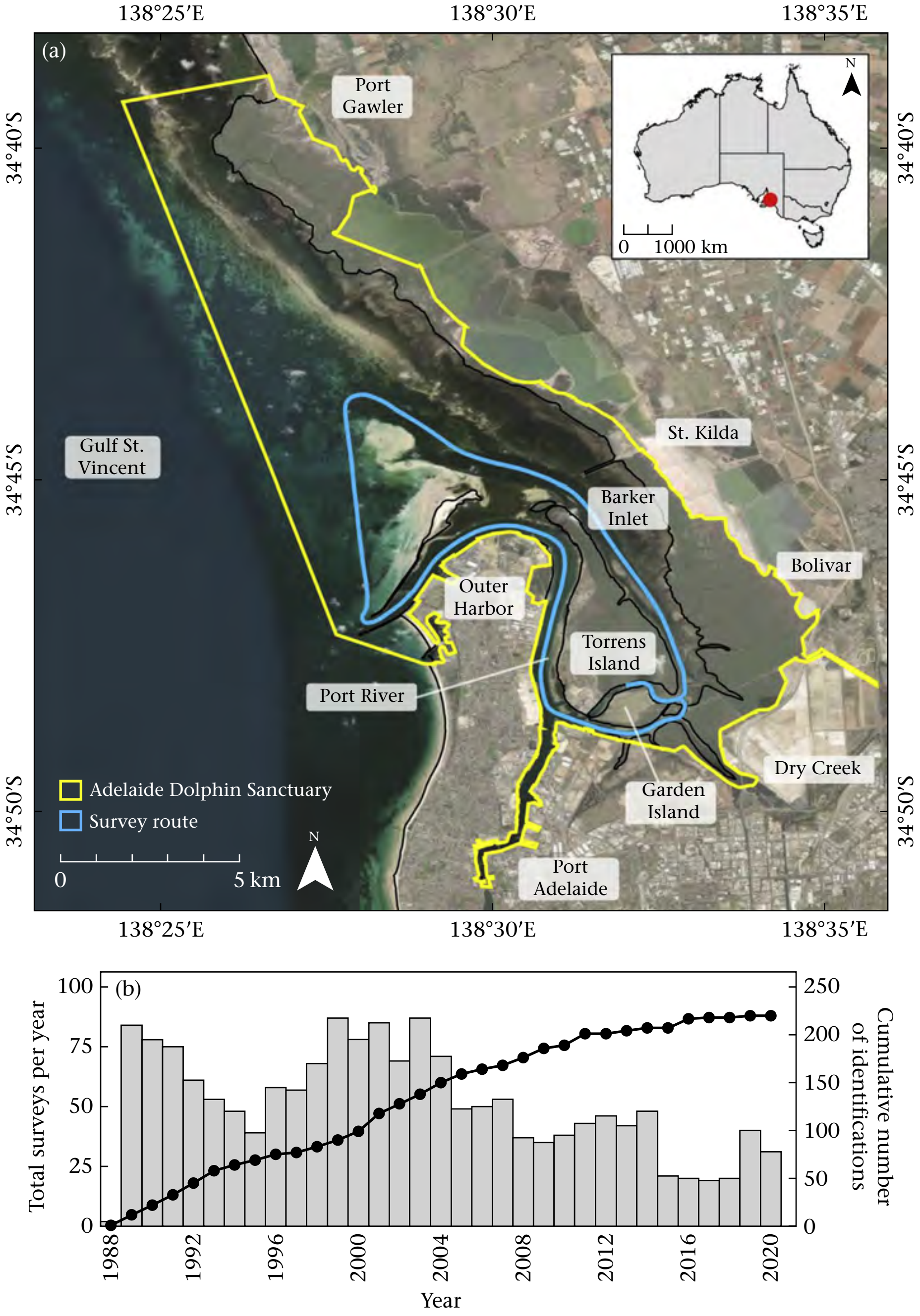

Figure 1. Study area and annual survey effort. (a) Map of the study area within the Adelaide Dolphin Sanctuary (yellow line), South Australia, and the survey route (blue line) followed by the research vessel to monitor Indo-Pacific bottlenose dolphins, *T. aduncus*, between 1988 and 2020; and (b) total number of boat-based dolphin surveys (grey bars) and cumulative number of dolphins identified (black line) per year. N.B. Cumulative number of dolphins identified excludes individuals where age was unknown.

Statistical Analyses

All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022). Test results are reported as the probability (P value) that the difference between groups was due to random chance, with the significance threshold set to $P < 0.05$. Measures of central tendency are reported as mean ± standard deviation. Data visualization was produced in R using ggplot2 (Wickham, 2016).

Sightings threshold for ranging pattern analysis

The reported minimum number of records required to estimate an animal's home range is highly variable between species, populations and algorithms used (e.g. Flores & Bazzalo, 2004; Urian et al., 2009). To determine the minimum number of sightings required to produce a robust estimation of a dolphin's range for this study region, we used an iterative method to calculate the representative range size (95% kernel) of each individual dolphin with an increasing number of sighting points (Urian et al., 2009). The representative range was used for this analysis (rather than the core range, 50% kernel) as it is less susceptible to small-scale variations in range size over time (e.g. seasonal changes). Dolphins with a large number of sightings (i.e. ≥100) during their adult years (≥10 years of age) were selected for this process. Sighting locations of individuals recorded as calves or subadults were excluded from this threshold analysis due to the high site fidelity of young dolphins to their natal group and/or area during this period (McHugh et al., 2011; Möller, 2012; Sprogis et al., 2016).

The R package adehabitatHR (Calenge, 2006) was used to estimate the representative range (95% kernel) size for each dolphin using a random subsample of sightings (kernelUD function parameters: bandwidth = 200 m; kernel function = bivariate; grid size = 500 × 500 pixels), with an outline of the study area used to account for physical barriers to dolphin movement. Each range size was calculated through an iterative, random subsampling process using from 10 to 150 sighting locations and repeated 100 times per individual dolphin and quantity of sightings. The threshold for a robust estimation of range size was determined by visual inspection of the area observation curve (i.e. plot of mean range size against the number of sighting points used in the range calculation; Laver & Kelly, 2008) and estimated to be the number of sightings at which the stepwise percentage change in range size became less than 5%. This study assumed that an individual's ranging pattern does not vary considerably over time, given that the minimum sightings threshold indicates when there is no significant change in range size for an individual. While this does not account for variations in range location, given the small and restricted nature of the study area, this study assumed that dolphins continued to use the same general area.

Estimation of individual ranging patterns

It has been recommended that numerical comparisons of ranging patterns in animals should focus on the core part of the range due to a lack of ability to accurately estimate ranges at the periphery of the data or study area (Seaman et al., 1999), and the suggested greater ecological importance of core areas of use. This study investigated differences in the size of both the core and representative ranges, and measures of spatial overlap of the core range only. Spatial calculations and visualization of dolphin core and representative ranges were conducted using ArcGIS Pro version 3.0.3 with the Spatial Analyst and Geostatistical Analyst extensions (ESRI, 2022), and the spatial reference set to WGS 1984 UTM Zone 54S.

For individual dolphins that met the estimated sighting threshold criteria, their core and representative ranges were calculated using a kernel density estimation method, accounting for coastlines and landmasses to avoid biases introduced by physical barriers to dolphin movement (Passadore et al., 2017; Sprogis et al., 2016). Settings of the kernel density estimation were kept consistent between individual dolphins to ensure comparable results (e.g. Worton, 1989). The bandwidth of 1000 m was chosen using an ad hoc method based on patterns of space use so that individual dolphins' ranges showed little fragmentation (e.g. Gitzen et al., 2006; Kie, 2013), and was not allowed to vary across the plane (fixed kernel method; for detailed parameters, see Table S2). The ‘representative range’ was defined as the 95% isopleth, which demonstrates the overall area used by an individual animal within the study region, and the ‘core range’ as the 50% isopleth, which represents the area most frequently used within the region (Fleming et al., 2019; Laver & Kelly, 2008; Worton, 1989). These ranges represent a minimum estimate of the daylight movement patterns of individual dolphins and only consider their space use across a two-dimensional plane. The core ranges of individual dolphins were then aggregated to identify which parts of the study region were most used as core areas.

Few previous studies have addressed the sensitivity of range estimations to the number of animal location points used in the calculation (Laver & Kelly, 2008), thus introducing potential bias to comparisons between ranges of individuals with differing numbers of location points. To address this concern, we used Kendall rank correlation to test the correlation between the number of sighting locations used to calculate a dolphin's range and the size of their representative and core ranges.

To assess whether the inclusion of nonadult sightings affected range estimation, we analysed the representative and core range sizes estimated using only sightings of adult dolphins compared to the representative and core range sizes estimated using all sightings (regardless of age) for each individual dolphin. This was to ascertain the validity of later comparisons with dolphins that were frequently observed, but primarily during calf and/or subadult phases.

Assessing differences in core and representative range sizes

We determined whether there were differences in the core and representative range sizes between individual dolphins according to: (1) sex (female, male), (2) vital status (alive, deceased), and (3) between recently deceased (2018–2022) dolphins and other dolphins assessed in this study (i.e. dolphins still alive in the study area, dolphins that died prior to 2018). To assess whether the observed differences in range sizes were not due to chance, randomization tests (with 100 000 iterations) were used to compare the observed metric (from either a Welch t test or ANOVA) against the expected values generated through a randomization resampling procedure (Manly, 1997). Following a significant Welch t test or ANOVA outcome, a post hoc Tukey HSD test was used to identify which specific groups were significantly different from each other.

Calculating spatial overlap of ranges

Spatial overlap of core ranges was assessed at both the population and individual levels. Population-level core range overlap was described using the general overlap index (GOI) developed by Ferrarini et al. (2021). The GOI ranges between 0 and 100, with GOI = 0 indicating no overlap and GOI = 100 indicating full overlap. GOI was calculated as:

$$\mathrm{GOI} = 100 \times \frac{\sum_{i=1}^{n} A_i - \bigcup_{i=1}^{n} A_i}{\sum_{i=1}^{n} A_i - \max(A_i)} \tag{1}$$

where $\sum A_i$ is the sum of range extents/areas; $\bigcup A_i$ is the union of range extents/areas; $\max(A_i)$ is the extent/area of the largest range; and n is the number of ranges under observation (Ferrarini et al., 2021).

To evaluate the degree of overlap at the individual level, the percentage overlap of core ranges was calculated for each pair of dolphins in a nonsymmetrical pairwise matrix arrangement. Percentage overlap was calculated as:

$$P_\mathrm{a} = 100 \times \frac{\mathrm{AO}_{\mathrm{a,b}}}{\mathrm{CR}_\mathrm{a}} \tag{2}$$

where P_a is the proportion of dolphin A's core range (CR_a) that is overlapped by the core range of dolphin B (CR_b); $\mathrm{AO}_{\mathrm{a,b}}$ is the area of overlap between CR_a and CR_b; and CR_a is the area of dolphin A's core range (Kernohan et al., 2001).

We investigated whether there were differences in core range overlap between individual dolphins according to: (1) sex (female, male), (2) vital status (alive, deceased), (3) body condition of recently deceased (2018–2022) dolphins (emaciated, unknown) and (4) between dolphins still alive in the study area, dolphins that died prior to 2018 and recently deceased (2018–2022) dolphins. To assess observed differences in core range overlap while accounting for the dyadic nature of the pairwise overlap data, we used generalized linear mixed models (GLMMs) for proportions with a beta error distribution and logit link function (Salinas Ruíz et al., 2023). These models considered if core range overlap varied among dyads according to the different levels of each fixed factor (i.e. sex, vital status, body condition). The models included random intercepts for dyad identity and individual dolphins to account for repeated measures within dyads and individuals. The models also accounted for potential zero inflation. We used the R package glmmTMB (Brooks et al., 2017) for model fitting. All GLMM results are presented on the logit scale (not the response scale), unless otherwise stated.

Association patterns and core range overlap

Dolphins live in a fission–fusion society with individuals showing different levels of preferred association (Connor & Krützen, 2015; Wang, 2018); such associations can lead to bias in estimates of core range overlap (Frère et al., 2010; Urian et al., 2009). To assess if association patterns among individual dolphins were correlated with spatial overlap in their core ranges, we first calculated a half-weight association index for each dolphin pair using SOCPROG version 2.9 (Cairns & Schwager, 1987; Whitehead, 2009). Calculation of the association index was restricted to dolphins with ≥10 sightings (excluding sightings as a dependent calf, 0–3 years). The threshold of 10 sightings was chosen to ensure accuracy in the association indices, as including individuals with fewer sightings may lead to inaccuracies (Bejder et al., 1998). The threshold of 10 sightings aligns with practices in other studies on dolphin social structure, ensuring robust data while allowing for comparability across research, and striking a balance between practical field constraints and the need for reliable data, accommodating typical study durations and recapture rates (Methion & Díaz López, 2019; Parra et al., 2011; Zanardo et al., 2016). The degree of correlation between the matrix of association indices and the pairwise core range overlap matrix was then determined using a Mantel test (Pearson product-moment correlation method and 999 permutations; Oksanen et al., 2022).

Ethical Note

This research was completed under the Research Permit E26931-1 from the Department of Environment and Water, South Australia. This study used observational methods to collect data on wild animals and adhered to local marine mammal approach distance guidelines (Government of South Australia, 2010) including: vessels must not move closer than 50 m, or 150 m if the animal is a calf; vessels within 150 m must not approach the animal head on or tail on, drop anchor or remain within 150 m for more than 60 min; and vessels must not move closer than 150 m if the animal shows signs of disturbance, appears to be sick, injured or entangled.

RESULTS

Survey Effort and Dolphin Sightings

Survey effort

Boat surveys occurred between 2 and 87 times per year ($X \pm SD = 51 \pm 22$, $N = 1692$; Fig. 1b), with an average of 12 dolphins sighted per survey ($X \pm SD = 12 \pm 8$, $N = 1692$). No significant bias in monthly survey effort was present (ANOVA: $F_{11,359} = 1.77$, $P = 0.057$), with an average of four surveys conducted each month ($X \pm SD = 4 \pm 3$, $N = 396$).

After removing sightings with inaccurate GPS coordinates, sightings of nonunique dolphins, any resighting of an individual dolphin within the same survey and sightings of dolphins whose age was unknown, the data set for analysis consisted of 13 256 sighting records and 220 unique individual dolphins photo identified across 33 years (1988–2020; Fig. 1b). On average, each dolphin was sighted 60 times ($X \pm SD = 60 \pm 96$, $N = 220$). Of the identified dolphins, 30.3% were female and 16.4% were male, while the sex of the remainder was unknown.

Sightings threshold for ranging pattern analysis

The change in mean representative range (95% kernel) size with respect to number of sighting locations showed that a minimum of 80 adult sightings were required to produce a robust estimation of a dolphin's range (Table S1). The inclusion of additional sighting locations above this threshold had a minimal effect on the range size, with a stepwise increase of <5% (Table S1). Previous studies have reported differences in the sightings threshold for male and female dolphins (e.g. Urian et al., 2009); however, the difference between sexes appeared to be negligible in this study (Table S1). Thirty-four individual dolphins (15% of individuals identified over the study period) met the threshold criteria of ≥80 sightings (excluding sightings as a dependent calf, 0–3 years), and there was no significant correlation found between the number of sighting locations used to calculate a dolphin's range and the size of either the representative range (Kendall rank correlation: $\tau = 0.14$, $N = 34$, $P = 0.236$) or the core range (Kendall rank correlation: $\tau = -0.06$, $N = 34$, $P = 0.604$; Fig. S1). Given the high number of sightings needed to estimate ranging patterns (≥80 per individual dolphin), the dolphins analysed in this study probably represent only the resident animals.

Comparison of dolphin ranging patterns using only adult sightings versus lifetime sightings

Of the 34 dolphins that met the threshold criteria (≥80 adult sightings), 15 individual dolphins (44%) had additional sightings recorded during their calf and/or subadult life stages (Table S4). Of these 15 dolphins, the number of adult sightings represented 33.4–99.8% of the lifetime sightings available for that individual ($X \pm SD = 68.7 \pm 24.8\%$, $N = 15$).

There were no significant differences between adult and lifetime representative range sizes (Welch *t* test: $t_{27.9} = -0.89$, $P = 0.382$) or core range sizes (Welch *t* test: $t_{25.9} = -0.71$, $P = 0.490$; Fig. S2). The adult core range of all dolphins, except one, overlapped their lifetime core range by at least 70%, showing little spatial change in core ranges over their lifetime. Overall, there was no substantial difference in core or representative range size, or substantial effect on core range spatial distribution when nonadult sightings were included in the range calculation, provided the number of sightings met the threshold criteria (≥80 sightings). Thus, when estimating individual dolphin ranges, all available sighting locations (excluding those recorded when the dolphin was a dependent calf, 0–3 years) were used in the calculations.

Dolphin Ranging Patterns in the Southern Adelaide Dolphin Sanctuary

Dolphin demographics

Applying the threshold criteria of ≥80 sighting locations to this data set resulted in 34 individual dolphins (e.g. 14 females, 20 males) that were suitable for analysis of ranging patterns in the study area (Tables 1 and S3). Of these, seven individual dolphins were currently alive (three females, four males) and 27 had died or were presumed dead (11 females, 16 males). Due to the longitudinal nature of this data set, the temporal occurrence of these individuals relative to each other was examined using their estimated year of birth and year of death/disappearance. During any one year of survey effort (1988–2020), an average of 72% of these individuals were present in the study area ($X \pm SD = 72.4 \pm 17.0\%$, $N = 34$; Fig. S3).

Table 1
Demographic details, number of sightings and range sizes of Indo-Pacific bottlenose dolphins, *T. aduncus*, that were used to estimate ranging patterns in the southern part of the Adelaide Dolphin Sanctuary

Dolphin ID	Sex	Vital status	Current age/age at death[d]	Subadult + adult sightings	Representative range size (km^2)	Core range size (km^2)
F001	F	Died	24	225	6.47	1.92
F005	F	Presumed dead[b]	31	198	24.25	4.79
F019	F	Died	19	86	16.97	2.57
F028	F	Died	35	153	15.31	2.14
F139	F	Alive	39	161	17.47	2.50
F200	F	Alive	37	544	18.60	2.17
F224	F	Died	22	146	12.73	2.35
F257	F	Presumed dead[b]	27	291	20.27	3.30
F328	F	Presumed dead[b]	27	98	15.34	2.96
F351	F	Presumed dead[c]	24	295	9.50	0.65
F367	F	Died	26	354	6.99	0.38
F377	F	Presumed dead[b]	21	165	8.82	1.39
F421	F	Presumed dead[c]	22	148	7.52	1.61
F435	F	Alive	19	172	5.85	0.61
M004	M	Presumed dead[c]	30	487	21.58	2.12
M008	M	Presumed dead[b]	24	151	22.47	3.51
M013	M	Died	34	439	26.20	2.98
M016	M	Died	32	237	24.72	3.73
M063	M	Died	24	136	19.30	2.90
M080	M	Died	23	135	19.70	2.69
M097	M	Presumed dead[b]	36	279	25.63	4.40
M149	M	Presumed dead[b]	26	256	23.70	3.30
M179	M	Presumed dead[b]	33	175	13.17	2.15
M209	M	Presumed dead[b]	34	158	19.80	3.29
M255	M	Alive	40	432	23.99	3.18
M329	M	Died	20	215	8.24	1.01
M389	M	Presumed dead[c]	20	308	6.66	0.29
U159	M[a]	Presumed dead[b]	26	94	11.55	2.41
U291	M[a]	Presumed dead[c]	25	144	18.36	3.69
U320	M[a]	Presumed dead[b]	23	86	8.34	1.34
U385	M[a]	Alive	24	141	11.26	2.16
U386	M[a]	Presumed dead[b]	22	140	8.38	1.47
U391	M[a]	Alive	20	191	12.55	0.89
U426	M[a]	Alive	26	96	13.60	2.44

[a] Dolphin assumed to be male based on long-term, consistent sightings without the presence of a calf.
[b] Dolphin disappeared from the study area for ≥2 years and was presumed deceased.
[c] Dolphin disappeared from the study area and was presumed deceased based on visible signs of illness (e.g. emaciation, severe wounds/scars) just prior to disappearance.
[d] For dolphins currently alive in the study area, age was calculated as of 2022.

Spatial distribution and range sizes of dolphins

The core ranges of most dolphins in the study area used for the analyses were located at the northern side of Garden Island (Angas Inlet; 62%; 21 dolphins), the northern section of the Outer Harbor channel (Light Passage; 62%; 21 dolphins) and along the Port River near the North Arm junction (53%; 18 dolphins; Fig. 2a and S4). The northern Barker Inlet was used as a core range by eight dolphins included in the analyses, and the entrance to Outer Harbor by ten individuals. On average, pairs of analysed dolphins shared 29.1% of their core range ($X \pm SD = 29.1 \pm 29.2\%$, $N = 1122$); however, the extent of spatial overlap between individuals was highly variable, ranging from 0% to 99.4%. The representative range (95% kernel) size of the 34 dolphins was from 5.9 to 26.2 km^2 ($X \pm SD = 15.4 \pm 6.5$ km^2, $N = 34$), with core areas of use (50% kernel) varying from 0.3 up to 4.8 km^2 ($X \pm SD = 2.3 \pm 1.1$ km^2, $N = 34$; Fig. 2b).

Comparison of dolphin ranges by sex

At the population level, there was a high degree of core range overlap between female and male dolphins (GOI = 78.7%). The population level overlap index among males (GOI = 78.9%) was higher than among females (GOI = 67.3%). The core ranges of the 14 female dolphins were relatively spread out within the study area, with only a slight preference shown for the northeastern side of Garden Island (Fig. 3a). Core ranges of the 20 male dolphins were concentrated around the Port River/North Arm junction and in Light Passage, with preference also shown for the northern side of Garden Island (Fig. 3b). On average, pairs of males showed greater overlap ($X \pm SD = 34.1 \pm 28.3\%$, $N = 380$) than pairs of females ($X \pm SD = 23.5 \pm 30.1\%$, $N = 182$) and mixed-sex pairs ($X \pm SD = 27.5 \pm 29.1\%$, $N = 560$), but the overlapping interquartile ranges suggested no significant differences (Fig. 3c). The GLMM, accounting for random effects of dyads and individual dolphins, revealed no differences in the core range overlap among female–female (GLMM: estimate ± SE = −0.621 ± 0.370, $Z = -1.679$, $P = 0.093$), female–male (GLMM: estimate ± SE = −0.086 ± 0.280, $Z = -0.308$, $P = 0.759$) and male–male pairs (GLMM: estimate ± SE = 0.104 ± 0.465, $Z = 0.223$, $P = 0.823$; Table S6).

Across the 14 female dolphins, representative ranges varied from 5.9 to 24.3 km^2 ($X \pm SD = 13.3 \pm 5.9$ km^2, $N = 14$) with core ranges between 0.4 and 4.8 km^2 ($X \pm SD = 2.1 \pm 1.2$ km^2, $N = 14$). The 20 male dolphins had representative ranges of 6.7–26.2 km^2 ($X \pm SD = 17.0 \pm 6.6$ km^2, $N = 20$), and core ranges of 0.3–4.4 km^2 ($X \pm SD = 2.5 \pm 1.1$ km^2, $N = 20$). The representative ranges of male dolphins were marginally larger than those of female dolphins (Welch *t* test: $t_{30.10} = -1.71$, $P = 0.104$), while their core ranges were similar in size (Welch *t* test: $t_{26.60} = -1.01$, $P = 0.310$; Fig. 3d and e).

Comparison of dolphin ranges by vital status over the whole study period

Population-level overlap suggests a near-complete overlap in core ranges between alive and deceased dolphins (GOI = 95.5%). The core ranges of the seven dolphins still alive in the study area showed no clearly defined hot spot (Fig. 4a). The core ranges of the 27 confirmed/presumed deceased dolphins were commonly

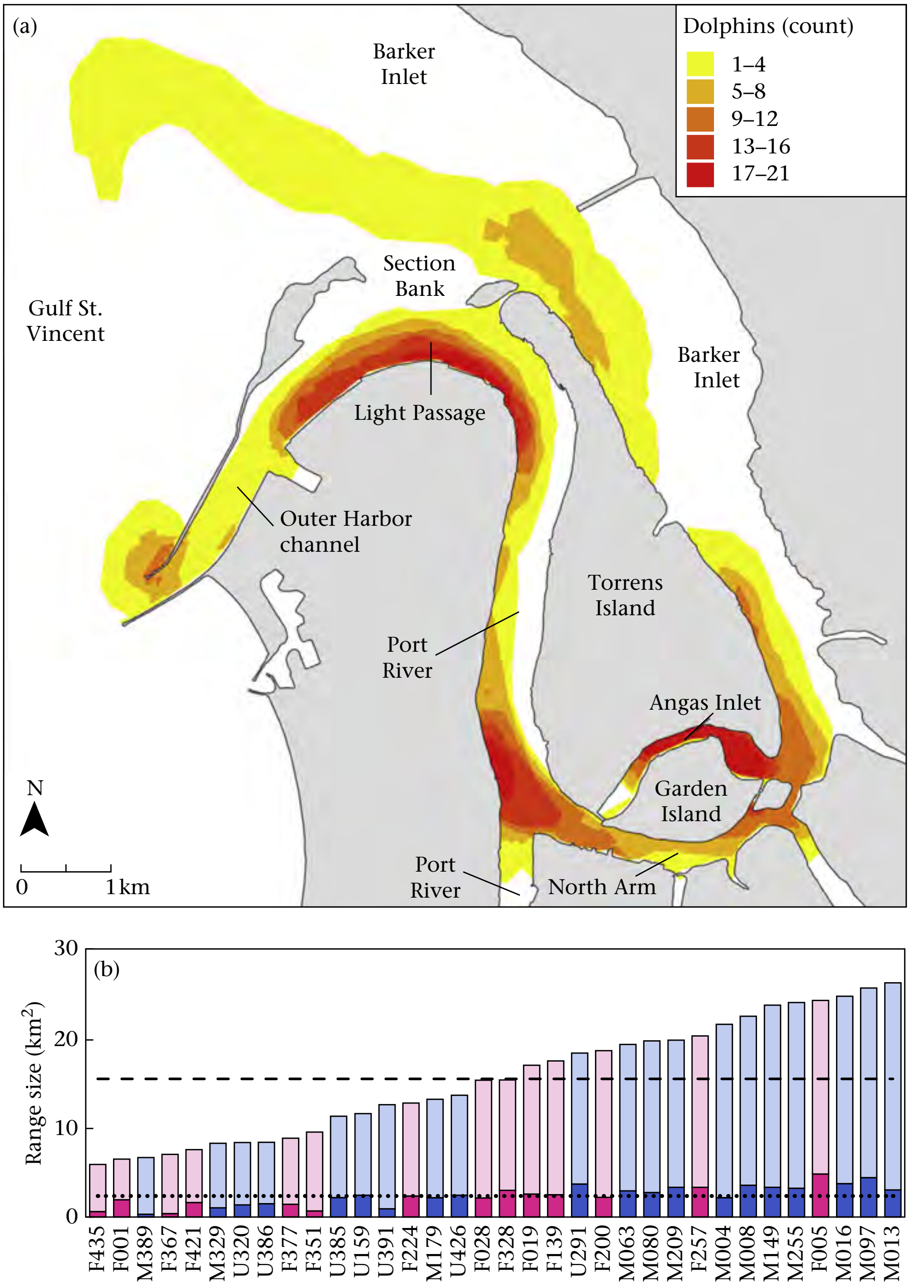

Figure 2. Spatial distribution of dolphin core areas of use and range sizes. (a) Aggregated core ranges (50% kernel) of 34 individual Indo-Pacific bottlenose dolphins, *T. aduncus*, (with ≥80 sightings) illustrating the intensity of use of different areas within the southern part of the Adelaide Dolphin Sanctuary. Yellow indicates areas used by only a few individual dolphins, while red represents hot spots of core ranges used by many individual dolphins. (b) Representative range (upper pale pink/blue bars) and core range (lower dark pink/blue bars) sizes. Range sizes of females are shown in pink ($N = 14$), and those of males in blue ($N = 20$). Mean representative range size (dashed line) and mean core range size (dotted line) shown.

situated in Angas Inlet, Light Passage and the Port River/North Arm junction (Fig. 4b). Although dolphins still alive in the study area had a lower average core range overlap between individuals ($X \pm SD = 26.1 \pm 34.7\%$, $N = 42$) than deceased dolphins ($X \pm SD = 29.3 \pm 28.6\%$, $N = 702$) and mixed pairs ($X \pm SD = 29.1 \pm 29.8\%$, $N = 378$), the overlap in their interquartile ranges suggested this difference was not statistically significant (Fig. 4c). The GLMM indicated no differences in core range overlap among dyads of currently alive dolphins (GLMM: estimate ± SE $= -0.566 \pm 0.571$, $Z = -0.990$, $P = 0.322$), dyads of currently alive and presumed/confirmed deceased dolphins (GLMM: estimate ± SE $= 0.054 \pm 0.434$, $Z = 0.124$, $P = 0.902$) and dyads of presumed/confirmed deceased dolphins (GLMM: estimate ± SE $= -0.129 \pm 0.617$, $Z = -0.210$, $P = 0.834$; Table S7).

Representative and core range sizes did not differ between currently alive dolphins and those that had died or disappeared from the study area (Welch *t* test: $t_{10.53} = -0.34$, $P = 0.756$; $t_{11.61} = -1.03$, $P = 0.379$; Fig. 4d and e). Dolphins that had died or were presumed deceased had representative and core ranges that were, on average, only 0.8 km^2 and 0.4 km^2 larger than those dolphins currently alive. Deceased dolphins (either confirmed or presumed) had representative range sizes between 6.5 and 26.2 km^2

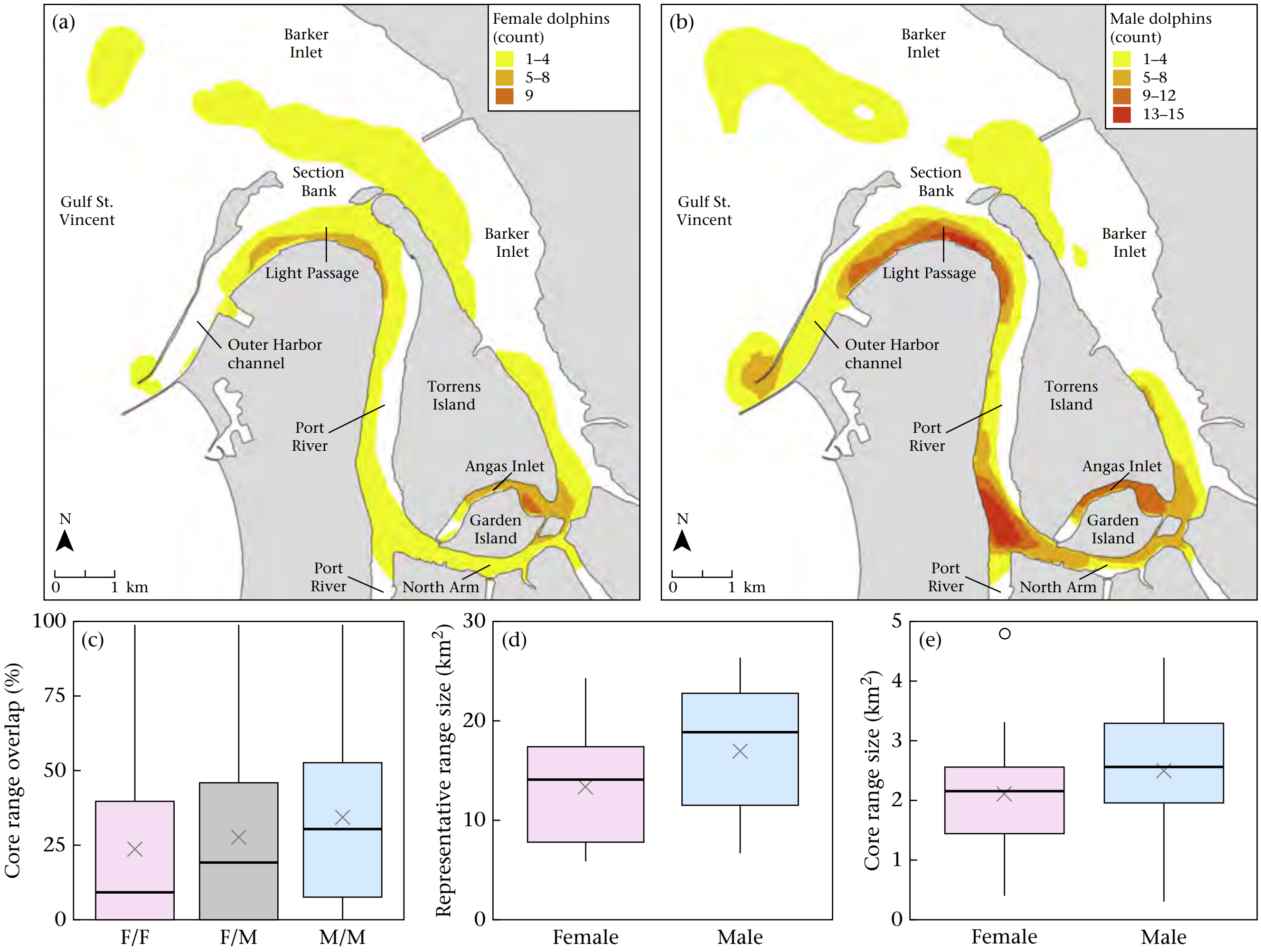

Figure 3. Spatial distribution of dolphin core areas of use and range sizes according to sex. Heat maps of aggregated individual core ranges (50% kernel) of 34 individual Indo-Pacific bottlenose dolphins, *T. aduncus*, with ≥80 sightings according to sex (14 female, 20 male) in the southern part of the Adelaide Dolphin Sanctuary showing the intensity of use by (a) female and (b) male dolphins, where red indicates areas more commonly used and yellow are areas used by fewer dolphins; (c) individual overlap of core ranges between pairs of dolphins where F = female, and M = male; (d) representative range sizes; and (e) core range sizes. Box plots indicate the interquartile range (box and whiskers), median (bold centre line), outlier (open circle), and mean (cross) values.

($X \pm SD = 15.6 \pm 6.7$ km^2, $N = 27$) and core range sizes from 0.3 to 4.8 km^2 ($X \pm SD = 2.4 \pm 1.2$ km^2, $N = 27$). The representative ranges of dolphins still alive in the study area varied between 5.9 and 24.0 km^2 ($X \pm SD = 14.8 \pm 5.8$ km^2, $N = 7$) and their core ranges between 0.6 and 3.2 km^2 ($X \pm SD = 2.0 \pm 0.9$ km^2, $N = 7$).

Correlation of dolphin core ranges and association indices

Individual association patterns and percentage of core range overlap between pairs showed a significant positive correlation (Mantel test: $r = 0.282$, $N = 34$, $P = 0.002$). The mean pairwise association index between dolphins ranged from 0 to 0.60 ($X \pm SD = 0.05 \pm 0.09$, $N = 1122$). The mean association index was higher for pairs of male dolphins ($X \pm SD = 0.07 \pm 0.13$, $N = 380$) than for female dolphins ($X \pm SD = 0.04 \pm 0.05$, $N = 182$). Eight pairs of males had an association index greater than 0.5, while the highest index for females was 0.3 (one pair).

Ranging Patterns of Recently Deceased Dolphins

Demographics of recently deceased dolphins

Thirteen dolphins died (confirmed deceased) or disappeared from the study area (presumed deceased) in recent years (2018–2022; Table 2). This group was comprised of six females and seven males, four of which had necropsy reports available (two females and two males). Reported circumstances of death for necropsied individuals included disease (two dolphins) and unknown (two dolphins; for category details, see Tomo & Kemper, 2022b). Where body condition was determined, either at death or prior to disappearance, seven dolphins were rated as emaciated. The number of sighting records per confirmed/presumed deceased dolphin, when they were alive, ranged from 92 to 354 ($X \pm SD = 178 \pm 85$ sightings, $N = 13$; Table S5). Age at death/disappearance ranged from 9 to 33 years ($X \pm SD = 20.3 \pm 6.7$ years, $N = 13$). The pattern of individual dolphins exhibiting acute changes in body condition (emaciation) prior to death or disappearing from the area also appears to affect younger age classes (e.g. Government of South Australia et al., 2021; The University of Adelaide, 2021; Tomo & Kemper, 2022a); however, some of these individuals were excluded from this study due to not meeting the ≥80 sightings threshold.

Spatial distribution and range sizes of recently deceased dolphins

For dolphins that were confirmed or presumed deceased between 2018–2022, Garden Island was the most common location

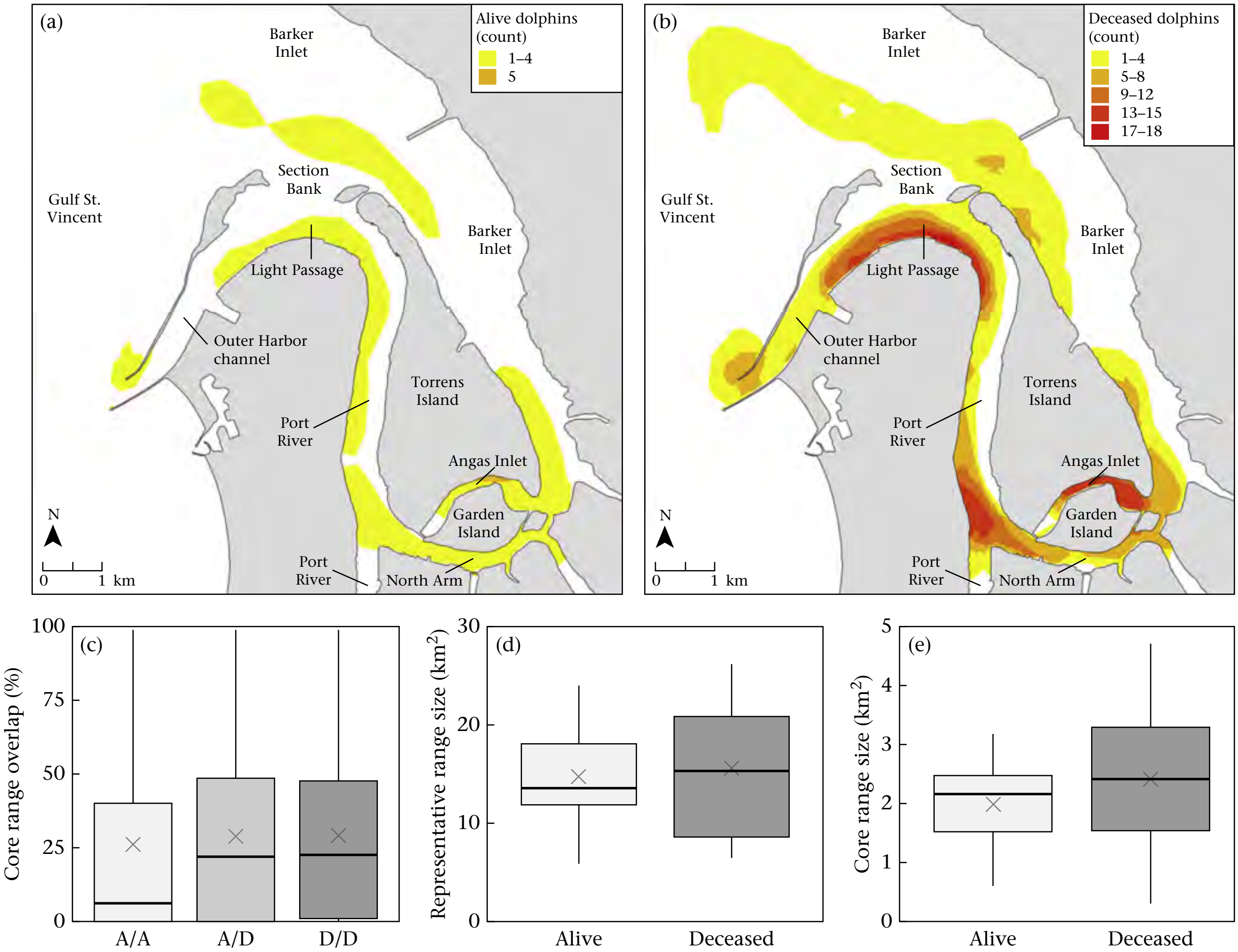

Figure 4. Spatial distribution of dolphin core areas of use and range sizes according to vital status. Heat maps of aggregated individual core ranges (50% kernel) of 34 individual Indo-Pacific bottlenose dolphins, *T. aduncus*, with ≥80 sightings according to vital status (seven alive, 27 confirmed/presumed deceased) in the southern part of the Adelaide Dolphin Sanctuary showing the intensity of use by (a) dolphins still alive in the study area and (b) confirmed/presumed deceased dolphins, where red indicates areas more commonly used and yellow are areas used by fewer dolphins; (c) individual overlap of core ranges between pairs of dolphins where A = alive and D = deceased; (d) representative range sizes; and (e) core range sizes. Box plots indicate the interquartile range (box and whiskers), median (bold centre line), outlier (open circle) and mean (cross) values.

for their core range (Fig. 5a and S5). Seventy percent of the recently deceased individuals (nine individuals) had part of their core range within the Garden Island area, with 38% (five individuals) having their entire core range completely within that area (Fig. 5a). Overall, dolphins that were confirmed or presumed deceased in recent years (2018–2022) had a representative range size between 2.5 and 20.3 km^2 ($X \pm SD = 9.3 \pm 5.2$ km^2, $N = 13$) and core ranges of 0.3–3.7 km^2 ($X \pm SD = 1.4 \pm 1.1$ km^2, $N = 13$; Fig. 5b).

Most of the seven dolphins that were emaciated at the time of death/disappearance had core ranges situated around Garden Island (six individuals; 86%), with five of these individuals having their core range located almost entirely on the northern side of the island in Angas Inlet (Fig. S6a). Half of the individual dolphins where body condition was unknown (three individuals) also had parts of their core range in Angas Inlet. However, unlike the emaciated individuals, these dolphins had larger core ranges, which expanded into other parts of the study area (Fig. S6b).

On an individual level, the average overlap between the seven emaciated individuals was 53.4% ($X \pm SD = 53.4 \pm 40.0\%$, $N = 42$), 24.6% among emaciated and unknown body condition individuals ($X \pm SD = 24.6 \pm 34.4\%$, $N = 84$) and only 13.2% between individuals with an unknown body condition ($X \pm SD = 13.2 \pm 23.3\%$, $N = 30$; Fig. S6c). The GLMM, accounting for random effects of dyads and individual dolphins, showed no significant differences in core range overlap among dyads of emaciated dolphins (GLMM: estimate ± SE = 0.430 ± 0.801, $Z = 0.537$, $P = 0.591$), emaciated and unknown body condition dyads (GLMM: estimate ± SE = -0.780 ± 0.771, $Z = -1.012$, $P = 0.312$) and unknown–unknown dyads (GLMM: estimate ± SE = -0.797 ± 1.437, $Z = -0.555$, $P = 0.579$; Table S8).

Ranging patterns of recently deceased dolphins compared to other dolphins in the population

On average, the representative range sizes of the 13 recently deceased (2018–2022) dolphins were significantly smaller ($X \pm SD = 9.3 \pm 5.2$ km^2, $N = 13$) when compared with other dolphins analysed in this study ($X \pm SD = 16.7 \pm 6.3$ km^2, $N = 26$; Welch *t* test: $t_{28.58} = 3.91$, $P = 0.001$; Fig. 6a). Similarly, the mean core range sizes of the recently deceased dolphins were also significantly smaller ($X \pm SD = 1.4 \pm 1.1$ km^2, $N = 13$) in comparison to other dolphins in this population ($X \pm SD = 2.5 \pm 1.1$ km^2, $N = 26$; Welch *t* test: $t_{22.71} = 3.05$, $P = 0.003$; Fig. 6b).

Range locations of the 13 recently deceased (2018–2022) dolphins were then compared to those of dolphins that died prior to

Table 2
Demographic details, number of sightings and range sizes of recently deceased (2018–2022) Indo-Pacific bottlenose dolphins, *T. aduncus*

Dolphin ID	Sex	Vital status	Year of death/ disappearance	Age	Circumstances of death/disappearance[e]	Body condition[e]	Subadult + adult sightings	Representative range size (km^2)	Core range size (km^2)
F367[d]	F	Died	2018	26	Unknown	Emaciated	354	6.99	0.38
M179[d]	M	Presumed dead[b]	2018	33	Unknown	Unknown	175	13.17	2.15
F384	F	Presumed dead[b]	2018	17	Unknown	Unknown	136	10.32	0.95
F461	F	Died	2018	16	Disease	Emaciated	94	8.51	1.34
F257[d]	F	Presumed dead[b]	2019	27	Unknown	Unknown	291	20.27	3.30
U386[d]	M[a]	Presumed dead[b]	2020	22	Unknown	Unknown	140	8.38	1.47
U291[d]	M[a]	Presumed dead[c]	2020	25	Unknown	Unknown	144	18.36	3.69
F377[d]	F	Presumed dead[b]	2020	21	Unknown	Unknown	165	8.82	1.39
M509	M	Presumed dead[c]	2021	9	Unknown	Emaciated	92	2.51	0.29
M389[d]	M	Presumed dead[c]	2021	20	Unknown	Emaciated	308	6.66	0.29
M501	M	Died	2021	12	Unknown	Emaciated	98	5.50	0.50
F421[d]	F	Presumed dead[c]	2021	22	Unknown	Emaciated	148	7.52	1.61
M513	M	Died	2022	14	Disease	Emaciated	170	3.60	0.27

[a] Dolphin assumed to be male based on long-term, consistent sightings without the presence of a calf.

[b] Dolphin disappeared from the study area for ≥2 years and was presumed deceased.

[c] Dolphin disappeared from the study area and was presumed deceased based on visible signs of illness (e.g. emaciation, severe wounds/scars).

[d] Dolphin was also included as part of the main group for analyses of dolphin ranging patterns in the study area.

[e] Circumstances of death for necropsied dolphins used categories set out by Tomo and Kemper (2022b), and body condition for presumed deceased individuals was based on field observations and photographic analysis.

2018, and to those currently alive in the study area to assess if there were spatial differences in the ranging patterns between these individuals. Overall, the primary location of the recently deceased dolphin core ranges (Garden Island/Angas Inlet; Fig. 5a) was shared with individuals that died prior to 2018 (Fig. S7) and with dolphins still currently alive in the study area (Fig. 4a). At the population level, there was an 85.8% overlap in the core ranges of dolphins currently alive, dolphins that died prior to 2018 and recently deceased (2018–2022) dolphins. The average core range overlap among these dolphins was similar, ranging from 26.1% among dolphins currently alive ($X \pm SD = 26.1 \pm 34.7\%$, $N = 42$) to 30.8% among those deceased prior to 2018 ($X \pm SD = 30.8 \pm 26.2\%$, $N = 342$) and 30.2% among recently deceased dolphins ($X \pm SD = 30.2 \pm 37.1\%$, $N = 156$; Fig. S8a). The GLMM, accounting for random effects of dyads and individual dolphins, demonstrated that there was no significant difference in the core range overlap among different combinations of dyads involving recently deceased (2018–2022) dolphins, dolphins that died prior to 2018 and those currently alive in the study area (Table S9).

Finally, there were clear differences found in representative and core range sizes of the 13 recently deceased (2018–2022) dolphins when compared to those of dolphins that died prior to 2018 ($N = 19$) and those currently alive in the study area ($N = 7$; ANOVA: $F_{2,36} = 7.25$, $P = 0.003$; $F_{2,36} = 6.13$, $P = 0.005$; Fig. S8b and c). On average, both the representative and core range sizes of recently deceased dolphins were significantly smaller than those of dolphins that died prior to 2018 (Tukey HSD: $P = 0.002$; $P = 0.004$) and somewhat smaller than those of dolphins still alive in the study area (Tukey HSD: $P = 0.139$; $P = 0.416$; Fig. S8b and c).

DISCUSSION

Characterizing the space use patterns of highly mobile marine species, such as dolphins, is challenging, but key to the conservation and management of species and populations. Using long-term photo ID data spanning 33 years, this study characterized the ranging patterns of individual Indo-Pacific bottlenose dolphins, *T. aduncus*, in the southern Adelaide Dolphin Sanctuary (ADS), a highly urbanized estuary in South Australia. Given the required number of sightings needed to estimate ranging patterns (≥80 per individual dolphin), the ranging patterns estimated are representative of only the resident dolphins in the study area. The results revealed dolphins resident to the study region do not use the area uniformly, with individuals differing in their spatial coverage and intensity of use and showing little spatial overlap (29%) between their individual core ranges. Core ranges were small (less than 5 km^2) and concentrated in three locations across the study area, with no apparent differences between females and males, or between dolphins still alive in the study area and those that were confirmed/presumed deceased. Interestingly, dolphins that were confirmed or presumed deceased in recent years (2018–2022) had core areas of use that were concentrated in a single, restricted region of the study area and were smaller when compared with other individuals in the population, highlighting a potential spatiotemporal aspect as a contributing factor in recent deaths.

Range Sizes of Delphinid Populations in Comparable Habitats

Comparisons between home range studies are often problematic due to differences in methodologies (e.g. minimum convex polygon or kernel interpolation) and parameters (e.g. bandwidth, number of sighting locations used), creating differing estimates of ranging patterns (Laver & Kelly, 2008; Oshima & Santos, 2016). When considering only studies that also used kernel methods to estimate ranges, the mean representative range size for the dolphins in this study was found to be similar to other inshore delphinid populations that live in comparable habitats (e.g. enclosed, shallow water depth, productive ecosystem, marine protected area), but were not necessarily the same species (*T. aduncus*, South Australia, Passadore et al., 2017; *Sotalia guianensis*, Brazil, Oshima & Santos, 2016; *S. fluviatilis*, Brazil, Flores & Bazzalo, 2004). Thus, our study adds to the evidence that dolphins in closed or restricted habitats are expected to have smaller ranges than those in open areas (Sprogis et al., 2016). In addition, individuals in habitats where resources are spatially and temporally predictable are expected to have smaller range sizes than in areas where resources are patchily distributed (Gowans et al., 2008). Resources such as prey abundance and predation risk are considered strong drivers of fine-scale changes in dolphin movement (Heithaus & Dill, 2002; Zanardo et al., 2016). Prey resources in the ADS were historically generally stable (Jackson & Jones, 1999), but have become less predictable in recent decades and need to be reassessed. Although, combined with low predation pressure (Steiner & Bossley, 2008), current prey availability may still limit the need for dolphins to range widely in search of prey in the ADS (Gowans et al., 2008).

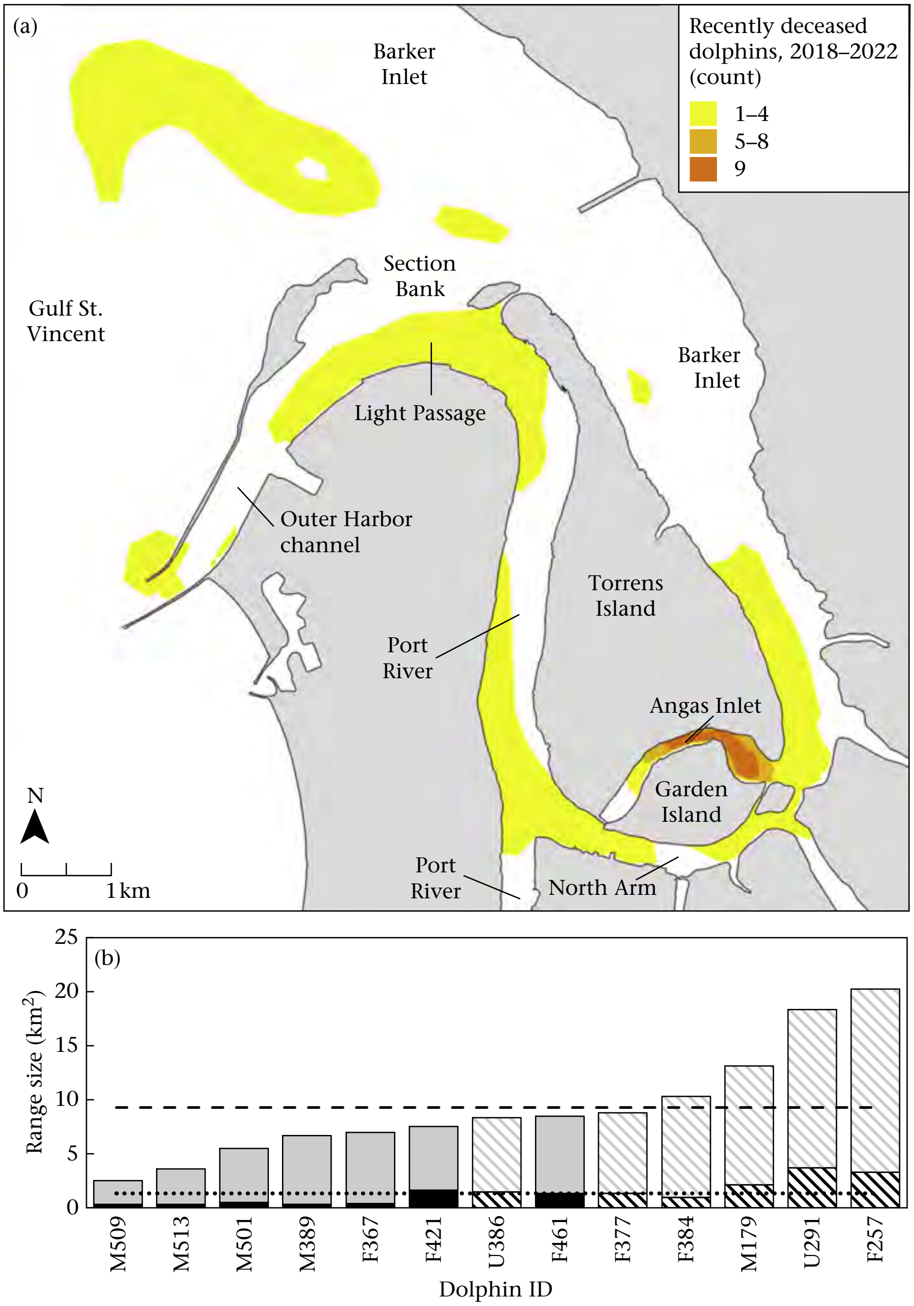

Figure 5. Spatial distribution of core areas of use and range sizes of recently deceased dolphins. (a) Aggregated core ranges (50% kernel) of 13 Indo-Pacific bottlenose dolphins, *T. aduncus*, confirmed or presumed to have died in recent years (2018–2022) within the southern part of the Adelaide Dolphin Sanctuary. Yellow indicates where only a few dolphins have their core range, while dark orange represents hot spots of common core ranges used by many recently deceased dolphins. (b) Representative range (upper grey bars) and core range (lower black bars) sizes for each individual dolphin. Individuals are rated as having an emaciated ($N = 7$; solid bars) or unknown ($N = 6$; patterned bars) body condition at death/prior to disappearance. Mean representative range size (dashed line) and mean core range size (dotted line) for recently deceased dolphins shown.

Variability in Animal Ranging Patterns

Variation in individual ranging patterns in a population can occur over fine or broad temporal scales and stem from biological differences (e.g. body condition, reproductive state, sex, age) and differing responses to environmental drivers or anthropogenic pressures (e.g. Grigione et al., 2002; McHugh et al., 2011; Tucker et al., 2014; van Beest et al., 2015). Given the nature of the data and the required number of sightings needed to estimate ranging patterns in our study area (≥80 per individual dolphin), our analysis focused on assessing differences in individual ranging patterns over a broad temporal scale (i.e. between 10 and 30 years of records depending on the individual dolphin).

Similarity in female and male dolphin range sizes, as shown in this study, has been documented in other small resident delphinid populations in Baía Norte, southern Brazil, and Coffin Bay, South Australia (Flores & Bazzalo, 2004; Passadore et al., 2017). Given their similar core and representative ranges and high degree of spatial overlap at the population level, we hypothesize that male and female dolphins have comparable resource requirements within the inner ADS (Gowans et al., 2008). It is important to note that due to data requirements for estimating individual range sizes

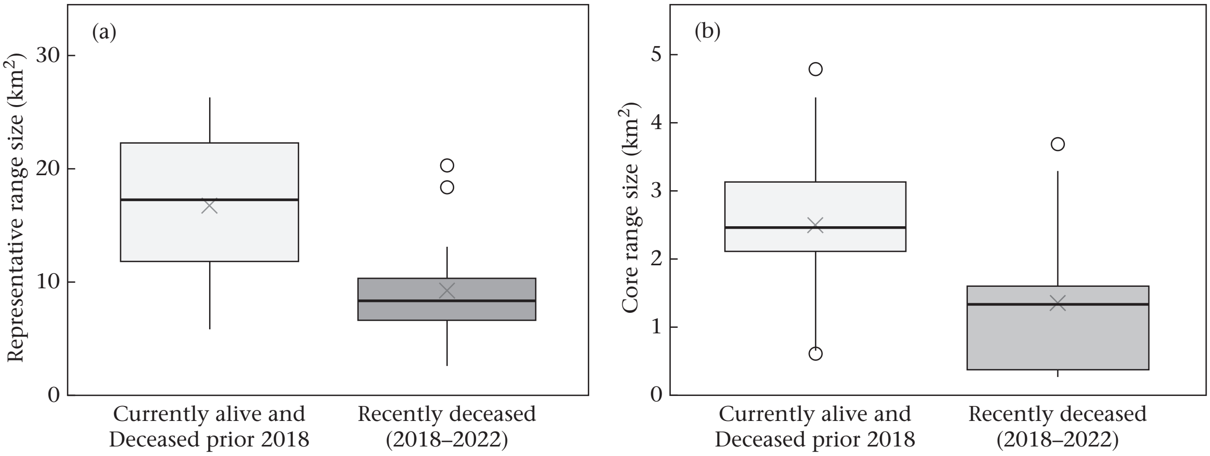

Figure 6. Range sizes of recently deceased dolphins compared with other dolphins in the population. Comparison of (a) representative and (b) core range sizes between recently deceased (2018−2022) individual dolphins (grey, $N = 13$) and other individual dolphins (currently alive and deceased prior to 2018, white, $N = 26$) in the southern part of the Adelaide Dolphin Sanctuary. Box plots indicate the interquartile range (box and whiskers), median (bold centre line), outlier (open circle) and mean (cross) values.

(i.e. ≥80 sightings) our analysis did not consider range size variation in relation to the mating season. It is possible that during the mating season, the average size of males' home ranges temporarily increases to overlap with a larger number of females and enhances their chances of mating with them (Möller & Beheregaray, 2004). Alternatively, if many females share a common ranging pattern, as is the case in this study, then males would not need a substantially larger range size to overlap with multiple females.

Within our study area, it appears core range overlap is dependent on association patterns, with males showing higher association indices and greater overlap. Male bottlenose dolphins (*Tursiops* spp.), often form long-term alliances with other males, which can help in securing access to females for mating (Connor et al., 2022; O'Brien et al., 2020). Higher overlapping core ranges among males may facilitate the maintenance of these cooperative partnerships, allowing frequent interactions necessary for alliance building and cooperative behaviours. Dolphins that share larger portions of their core ranges are more likely to encounter one another frequently, leading to stronger social bonds, possibly because they exploit similar resources or share critical habitats like resting or breeding areas (O'Brien et al., 2020). This spatial proximity fosters opportunities for cooperative behaviours, such as foraging or predator avoidance, and maximizing reproduction (Connor et al., 2022). Within our study area, we also observed a high degree of spatial overlap between males and females at the population level that may, in part, be a contributing factor to the high inbreeding observed in the population (Keep, 2022), which can contribute to weakened immunity and reduced disease resistance (Frankham et al., 2010). However, dolphins' social structure is not solely dictated by spatial overlap; individual preferences, kinship and social hierarchies also play significant roles (Frère et al., 2010). Future studies examining association patterns among bottlenose dolphins in the ADS should focus on the interplay between spatial overlap, individual preferences and kinship to better unravel the complexities of their social structure.

Animal Ranging Patterns in Urbanized Environments

Just under half of the recently deceased dolphins assessed in this study had a small (<1 km^2) core area of use concentrated in one single area of the study region (i.e. Angas Inlet). Furthermore, our results indicated that dyads of recently deceased dolphins with emaciated body condition exhibited the highest predicted core range overlap (60.6% when back-transformed), compared to emaciated−unknown (31.4%) and unknown body condition (31.1%) dyads. This pattern suggests that dolphins that die in an emaciated condition may preferentially utilize the same core areas, potentially due to shared habitat requirements or constraints linked to their body condition. Such spatial overlap may reflect aggregation in areas with limited resources or reduced ability to disperse due to compromised health. However, it is important to note that the small sample size of emaciated individuals in this study, combined with the uncertainty surrounding these estimates, resulted in a lack of statistical significance. These limitations emphasize the need for future studies with larger sample sizes to more robustly investigate whether the observed trend is consistent across dolphins with different body conditions. Most of the recognized stressors present in Angas Inlet (e.g. vessel traffic, recreational fishing, industrial outflows, terrestrial runoff, leaching of legacy pollutants from sediments) also occur elsewhere in the study area (Kirkwood et al., 2022), and thus dolphins with core areas of use in other areas (including individuals that are still alive) would be exposed to a similar stressor profile as the recently deceased dolphins. However, the intensity of exposure to these stressors is likely to be higher for the recently deceased dolphins due to their small core ranges. Additionally, prey toxicology studies have shown greater levels of contaminants such as persistent organic pollutants (e.g. polychlorinated biphenyls, PCBs; perfluorooctanesulphonate, PFOS) and heavy metals (mercury) in pelagic fish species inhabiting the Garden Island/Angas Inlet and Port River/North Arm core areas compared to the Light Passage core area or in waters outside of the Adelaide Dolphin Sanctuary (Wallace, 2023). In coastal Georgia, U.S.A., major point sources of PCBs within a localized environment were also found to be related to high persistent organic pollutant levels in the blubber layers of the resident dolphins (Balmer et al., 2011). The dolphins' small core ranges, coupled with heightened exposure to stressors at certain times and higher prey contaminant loads in the Angas Inlet area, may contribute to increased mortality among dolphins frequenting this core area of use.

Given that the dolphins analysed in this study probably represent resident animals it is conceivable that their knowledge and familiarity with the environment outside their local home range is limited (Mason et al., 2016), and that they are less likely to shift their range in response to changes in their habitat (either natural or anthropogenic; e.g. Wells et al., 2017). While unhealthy dolphins may be less likely to detect changes in environmental cues (e.g.

decreased prey availability) or threats (e.g. vessel traffic) and avoid them, some threats, such as bioaccumulated toxins, are unlikely to be detected by even healthy dolphins (Kirkwood et al., 2022). The continued use of an area such Angas Inlet where an animal's fitness is lowered in comparison to an alternative area may be considered an ecological trap (Hale & Swearer, 2016). An ecological trap may occur when there is high site fidelity or long-term residency (i.e. indicating an area of high habitat suitability) combined with high anthropogenic mortality (Atkins et al., 2016), which are all evident in the ADS dolphin population.

Implications for Conservation Management in the Adelaide Dolphin Sanctuary

Identifying core habitat areas used by marine wildlife in urbanized marine environments is essential for directing conservation and management efforts more effectively. In this study, all three identified core areas of use for resident dolphins overlap with one or more human activities (i.e. recreational boating and fishing, commercial shipping operations, industrial outflows, terrestrial runoff). Most activities are present in some form in all the three core areas of use; however, only the Outer Harbor and Port River/North Arm areas experience dredging and movement of large commercial vessels, and only the Garden Island area has a thermal effluent outflow and poor water circulation and flushing (Kirkwood et al., 2022). The impact on dolphin health of these potential stressors is likely to be different for each activity. For example, terrestrial runoff (including stormwater) can introduce pathogens into the marine habitat and increasing global temperatures have been shown to reduce immune function in some species (Collier et al., 2022). Vessel traffic and the associated noise pollution can affect the energy budget of marine mammals, such as disturbing the vital nursing time of calves, masking social communications (Bejder et al., 2019) or reducing the complexity of behaviours, which is an indicator of stress (Collier et al., 2022). However, even short-term periods (i.e. days) of significantly lower vessel traffic and noise can aid in decreasing marine mammal stress levels (Collier et al., 2022).

This study has identified Angas Inlet as an area heavily used by individual dolphins that have died or disappeared from the study area in recent years. It is likely that either the type, combination or intensity of stressors present in this area are contributing to the declining health of dolphins that spend most of their time here. At present, the apparent increase in dolphin mortalities during 2018–2022 appears to have ceased. This supports the likelihood that there was both a temporal and spatial consideration to the increase in dolphin mortalities. In addition to continuing the monitoring of the ADS dolphin population and conducting necropsies of deceased dolphins, a three-fold approach is recommended to reduce the cumulative effect of potential stressors on dolphins using Angas Inlet as a core area: (1) targeted research of direct and indirect pathways of potential dolphin stressors such as prey toxicology and water and sediment quality monitoring associated with dolphins core areas of use and adjacent areas in the ADS; (2) dolphin education and awareness campaigns concentrated towards users of Garden Island (e.g. influences of fishing and boating activities and of marine litter on dolphin behaviour and how these can lead to health complications), with the potential for spatial restrictions to anthropogenic activities in this core area of use and; (3) based on targeted research outcomes, focused environmental remediation efforts in Angas Inlet to detect the potential build-up of contaminants stemming from poor natural flushing of the estuary (Weijs et al., 2020).

CONCLUSION

Defining animal space use for populations living in urban environments can guide present and future research efforts into potential factors contributing to apparent population declines. The dolphin population in the southern part of the Adelaide Dolphin Sanctuary has core ranges that vary in size and spatial coverage among individuals, but show no apparent difference in range size or location between sexes. Recent dolphin mortalities in the area occurred mainly among dolphins that used a small, restricted region around Garden Island. Natural and anthropogenic stressors associated with this area, both spatially and temporally, may be responsible for the increase in dolphin mortalities and thus require further investigation. This study demonstrates the importance of long-term monitoring data for estimating ranging patterns of long-lived, highly mobile animals and identifying potential risks associated with their space use.

Author Contributions

Michelle Newman: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Mike Bossley:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Ryan Baring:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Luciana Möller:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Aude Steiner:** Writing – review & editing, Data curation. **Guido J. Parra:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Formal analysis, Conceptualization.

Data Availability

The data underlying this article cannot be shared publicly due to legal restrictions. We have a legal obligation under the terms of the agreement with the author of the raw data. This obligation prohibits us from publishing or making the raw data publicly available.

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

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