

Coastal dolphins and marine megafauna in Exmouth Gulf, Western Australia: informing conservation management actions in an area under increasing human pressure

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ABSTRACT

Context. Exmouth Gulf is adjacent to the Ningaloo Marine Park, a UNESCO-listed area in Western Australia. The gulf remains largely unprotected, and is under increasing anthropogenic pressure from proposed industrial activities that pose threats to marine megafauna inhabiting the gulf. Threatened and near threatened species, such as the Australian humpback dolphin (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), reside in the gulf; however, detailed information on their ecology and behaviour is lacking. **Aims.** The aim was to (1) provide baseline data on the distribution, encounter rate, group size and behaviour of coastal dolphins over an area where current industrial developments are proposed, and (2) report on the occurrence of other marine megafauna within this area. **Methods.** Boat-based photo-identification surveys were conducted on the western coastline of Exmouth Gulf along pre-determined line transects (150 km²) over austral autumn/winter 2021. **Key results.** Across 809.35 km of surveyed waters (181 h), a total of 93 bottlenose dolphin, 15 humpback dolphin, and six interspecific dolphin groups were sighted. Bottlenose dolphin groups were encountered at a rate of 0.077/km, humpback dolphin groups at 0.015/km and interspecific dolphin groups at 0.005/km. Dolphins were predominantly recorded in shallow (mean 10 m) and warm (mean 21°C) waters, and were commonly travelling and foraging. In total, 199 individual bottlenose dolphins and 48 humpback dolphins were photo-identified (excluding calves). There were 30 bottlenose dolphin calves (including three newborns) and four humpback dolphin calves (including two newborns) identified. Other marine megafauna group sightings included humpback whales (*Megaptera novaeangliae*; $n = 32$), southern right whales (*Eubalaena australis*, $n = 1$), dugongs (*Dugong dugon*, $n = 25$), turtles ($n = 54$), sea snakes ($n = 27$), manta rays (*Mobula alfredi*, $n = 13$) and sharks ($n = 2$). **Conclusions.** The presence of threatened marine species feeding, socialising, and resting highlights the importance of these waters for the identified species. **Implications.** The information provided is applicable for the spatial management and conservation efforts of these species, and aids in informing environmental impact assessments of individual and cumulative pressures.

Keywords: boat-based surveys, bottlenose dolphin, distribution, encounter rate, humpback dolphin, interspecific groups, *Sousa sahulensis*, *Tursiops aduncus*.

Introduction

Three species of coastal dolphins have been recorded in Exmouth Gulf, Western Australia (WA), the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*, herein bottlenose dolphin), Australian humpback dolphin (*Sousa sahulensis*, herein humpback dolphin), and the Australian snubfin dolphin (*Orcaella heinsohni*; Allen *et al.* 2012; Brown *et al.* 2012). Bottlenose dolphins are found in tropical and temperate coastal waters in the Indian Ocean and the western Pacific Ocean (Wang 2018). The humpback dolphin is distributed throughout the tropical waters of southern Papua New Guinea and northern

Australia until ~22–23°S latitude (Parra *et al.* 2004; Mendez *et al.* 2013; Jefferson and Rosenbaum 2014). Snubfin dolphins are found in the tropical waters of southern Papua New Guinea and northern Australia until ~18°S (Parra *et al.* 2002; Beasley *et al.* 2005; Brown *et al.* 2016). Each species is typically found in shallow, coastal waters in small populations of <150 individuals, with individuals displaying small ranging patterns (<300 km²) and moderate to high levels of site fidelity (Parra *et al.* 2006; Brown *et al.* 2016; Sprogis *et al.* 2016). Because of their small population sizes, their biological characteristics, and the overlap in their coastal distribution with anthropogenic developments, humpback and snubfin dolphins are listed as Vulnerable (Parra *et al.* 2017a, 2017b) and bottlenose dolphins as Near Threatened (Braulik *et al.* 2019) on the IUCN Red List of Threatened Species. These species are protected in Australian waters under the *Environment Protection and Biodiversity Act* (EPBC Act 1999), and humpback and snubfin dolphins as priority fauna in WA (*Western Australia Biodiversity Conservation Act* 2016).

Exmouth Gulf is a large embayment in north-western Australia characterised by shallow (<20 m) and highly turbid waters. Exmouth Gulf neighbours the renowned Ningaloo Reef, which is a part of the UNESCO Ningaloo Coast World Heritage Area (UNESCO 2011). The Ningaloo Reef ecosystem is inherently connected and ecologically linked with Exmouth Gulf (EPA 2021). The gulf hosts a large diversity of estuarine intertidal habitats and mangrove forests that provide nutrient-rich waters for a large variety of marine invertebrate and vertebrate species (Fitzpatrick *et al.* 2019; EPA 2021; Sutton and Shaw 2021). The gulf was originally included in the recommended optimal UNESCO Ningaloo Coast World Heritage area listing; however, the final boundary excluded the majority of the gulf, leaving it unprotected (WHCC 2005; UNESCO 2011).

The distribution of dolphins in Exmouth Gulf has been opportunistically assessed through humpback whale (Jenner and Jenner 2005; Irvine and Salgado Kent 2019) and dugong aerial surveys (Preen *et al.* 1997; Hodgson 2007; Hanf *et al.* 2022). However, these flights were not designed specifically as dolphin surveys, and subsequently dolphins were counted secondarily to the focus species, may have been missed/misidentified, or not identified to species level (Preen *et al.* 1997; Hanf *et al.* 2022). In the most recent aerial survey over Exmouth Gulf, 179 dolphin groups (species not identified) were sighted opportunistically, indicating that dolphins occur throughout most of the gulf, with the highest density in the north-western section (Irvine and Salgado Kent 2019). Dedicated boat-based dolphin surveys around the top of the peninsula, the North West Cape, which separates Exmouth Gulf from the Indian Ocean, reported large numbers of humpback and bottlenose dolphins inhabiting these waters, and that their ranging patterns are likely to extend into Exmouth Gulf (Hunt *et al.* 2017; Haughey *et al.* 2020).

North-western Australia has been an area of rapid development through the expansion and exploration activities of the mining and petroleum industries. Such rapid development has raised concerns about the potential impacts of human activities on threatened and near threatened dolphin species (Allen *et al.* 2012; Bejder *et al.* 2012; Hanf *et al.* 2016). Exmouth Gulf sustains the Exmouth Gulf Prawn Managed Fishery, holds mining and exploration leases and is under increasing pressure from industrialisation. Exmouth Gulf has experienced rejected or discontinued proposals for construction of evaporative salt ponds for salt mining, service wharfs, shipping channels, large-scale prawn aquaculture, and oil and gas facilities. Although there are rejected proposals, future industrialisation is currently proposed, including the construction of a deep-water port on the western coast of the gulf (EPA 2021; Sutton and Shaw 2021). The deep-water port proposal is for moorings suitable for cruise ships, cargo ships, naval vessels, oil and gas servicing vessels, and agriculture ships, and requires a channel to be dredged to support these large ships (EPA 2021). Information on the ecology and behaviour of coastal dolphins in Exmouth Gulf, including along the western coast where coastal development is proposed, is lacking. As a result, industry as well as State and Commonwealth Government agencies do not have the information required to make informed decisions about the potential impacts of proposed development activities on these species.

In this study, we aimed to collect information on the distribution, encounter rate, group size and behaviour of coastal dolphins on the western coastline of Exmouth Gulf. Boat-based photo-identification surveys were conducted along pre-determined transect routes, which were consistent with transects surveyed for dolphins around the North West Cape (Haughey *et al.* 2020, 2021; Hunt *et al.* 2017, 2019, 2020). Data were also collected on the occurrence of other marine megafauna of interest, including whales (mysticetes), dugongs (*Dugong dugon*), turtles (Chelonioidae), sea snakes (Hydrophiinae), manta rays (*Mobula alfredi*) and sharks (elasmobranchs). The information provided intends to inform future environmental impact assessments, conservation management decisions and guide future research priorities.

Materials and methods

Study area

Exmouth Gulf is a large embayment (~2600 km²) with shallow waters (<20 m) that is dominated by wave and tide action (Brunskill *et al.* 2001; Lebrec *et al.* 2021; Fig. 1). The gulf is generally highly turbid (McKinnon and Ayukai 1996; Cartwright *et al.* 2021), partially due to a strong tidal surge, with a 2.5 m tidal range flowing at 1–2/m/s on a semi-diurnal regime (Semeniuk 1993; Taylor and Pearce 1999). The gulf is hypersaline, with salinity ranging from ~36 to

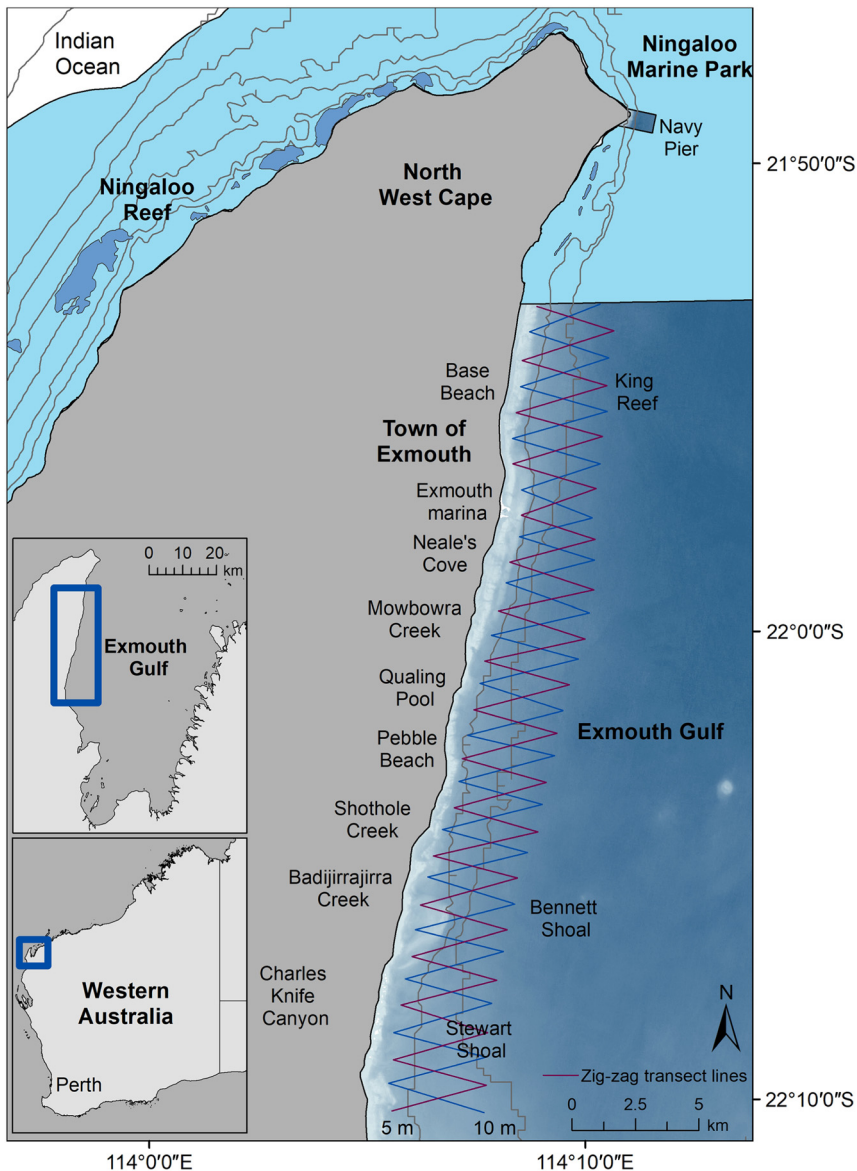


Fig. 1. The study area in Exmouth Gulf, Western Australia (insets), showing the transect design (dark blue and purple zig-zag lines) used to conduct boat-based surveys for dolphins and marine megafauna on the western coast of Exmouth Gulf. The solid light blue shaded area is the UNESCO Ningaloo Coast World Heritage Area along the Ningaloo Reef (patches displaying the fringing reef). Shallow areas along the coast were too shallow to access at times (e.g. during spring tides). Bathymetry displaying shallow waters (pale blue) and deeper waters reaching 20 m (darker blue; Lebrek *et al.* 2021).

38.5, with greater salinities occurring further south into the gulf (McKinnon and Ayukai 1996). The benthic habitat type consists of seagrass, macroalgae, reef (i.e. corals, sponges), sand/silt, mud and tidal flats (Lyne *et al.* 2006; Twiggs and Collins 2010; Loneragan *et al.* 2013). The region has a semi-arid tropical climate, with wet, hot summers and dry, mild winters. The gulf is dominated by biological noise (e.g. snapping shrimp, wave action; Sprogis *et al.* 2020), although it has more anthropogenic noise contributions from vessels (recreational and commercial) off the Exmouth marina (Bejder *et al.* 2019).

Boat-based data collection

Data were collected in the cooler months from May to July 2021 (austral autumn/winter). Boat-based photo-identification surveys were conducted along pre-determined

line transects along the western coast of Exmouth Gulf, covering an area of approximately 150 km² (Fig. 1). Surveys were completed in good weather conditions (i.e. <15 kn winds, Beaufort sea state of ≤3 and no precipitation). A small research vessel (5.8 m aluminium centre console, 100 hp four-stroke outboard) was used to collect data, and departure was from Exmouth Marina (21°57'S, 114°08'E). Transects consisted of zig-zag lines along a straight-line distance of ~33 km between the boundary of the Ningaloo Marine Park in the north and past Stewart Shoal in the south (Fig. 1). Transects extended 4–5 km adjacent to the coast. Transect segments were ~3.5 km in length (~115 km in total length) and evenly spaced (~2 km apart) to maintain equal coverage across the study area. Alternate mirrored transects were surveyed to obtain a broader coverage of benthic habitat type across the study area (MacLeod 2010).

The survey area covered waters <20 m deep. Transect lines were designed to match dedicated boat-based dolphin surveys conducted around the tip of the North West Cape (~120–130 km²) from 2013 to 2015 (Hunt 2018; Hunt *et al.* 2019, 2020; Haughey *et al.* 2020) and in 2018–2019 (Haughey 2021; Haughey *et al.* 2021). In this study, transect lines were the same from Ningaloo Marine Park boundary to Exmouth Marina (~8.5 km stretch) as Hunt and Haughey (Hunt 2018; Haughey 2021) to ensure that data were collected during 2021 around Exmouth Marina where vessels transit in and out of the marina channel. Transects continued from Exmouth Marine south for an additional ~25.5 km of coastline to include gulf waters that had not been systematically surveyed.

Whilst on transect searching for dolphins (on-effort data), the vessel was driven at slow speed (5–6 kn, 10 km/h). Three to four crew members were on board at all times. Two researchers scanned for dolphins ~250 m on either side of the vessel with the naked eye and occasionally binoculars (Bushnell 10 × 42), and the driver scanned ahead and around the vessel. Once dolphins were sighted, the effort was paused, and the dolphins were slowly approached to ~50 m to collect data. When off-transect, data were also opportunistically collected (off-effort data). Data collected included the species (bottlenose dolphin, humpback dolphin, or interspecific groups), location (latitude/longitude), time of day, group size (minimum, maximum, best estimate), age composition (calf, juvenile, adult), predominant behavioural state (i.e. behavioural state in which >50% of individuals in a group were involved; Table 1), general group cohesiveness (tight <2 m, medium 2–5 m, spread >5 m), and

environmental variables (water depth, water temperature, benthic habitat type, turbidity). The water depth and water temperature were taken from the boat's depth sounder, benthic habitat type was assessed visually by naked eye when the bottom was visible, and turbidity was measured with a secchi disc. Other marine megafauna, including whales, dugongs, turtles, sea snakes, manta rays and sharks were opportunistically recorded. The location, number of individuals, behaviour, direction of travel, water temperature and depth were noted. Species were identified on the basis of physical features (i.e. colour, size) and, where possible, photographs were taken to confirm species identification.

A group of dolphins was defined as one or more dolphins within 100 m of other members predominantly involved in the same behavioural state (Irvine *et al.* 1981; Wells *et al.* 1987). Associations of dolphins with two or more species were defined as interspecific groups, in which interactions could be positive, negative or neutral. Age classes were distinguished on the basis of behavioural cues and visual assessment criteria; adults were approximately >2 m in length, and calves <2/3 length of an adult swimming in close association with an adult, regularly besides or slightly behind an adult (Mann *et al.* 2000; Parra *et al.* 2006; van Aswegen *et al.* 2019). Calves were likely to be from 0 to 4 years of age, after which the majority of calves are weaned (Mann *et al.* 2000). Newborn calves were also classified to quantify the number of dolphins that were recently born (i.e. up to 3 months old). Newborns were small in length (<110 cm; van Aswegen *et al.* 2019), had fetal folds (vertical lines on the body from being compacted *in utero*), were popping out of the water when surfacing, often displayed

Table 1. Behavioural state definitions used to assess the predominant behavioural state (i.e. behavioural state in which >50% of the individuals in a group are involved) of dolphin groups encountered during boat-based surveys in Exmouth Gulf (Baker *et al.* 2017; Shane 1990).

Behavioural state	Definition
Foraging	Dolphins exhibit dives (tail-up and peduncle dives), indicating deeper excursions with multiple or single breaths, diving in different directions, or dolphins exhibit fast surfacings, erratic accelerations rooster tailing and fish chasing (e.g. snacking on their backs). Occasionally prey can be observed from the surface or jumping out of the water, and direct indication of feeding is when the prey is captured in the dolphin's mouth. On occasion, seabirds forage in the same vicinity as the dolphins indicating the foraging state of the dolphins.
Milling	Dolphin movements slow and with no apparent direction. Dolphins surface in different directions, resulting in no net movement. Group spacing varies. Activity level is low. Dive intervals are variable but short, diving angles are shallow.
Resting	Dolphins slow and steady in nature, and observed generally in a tight group. The group may take multiple breaths before diving and spending longer periods of down times in roughly the same area. Individuals may also rest on the surface like a log (known as snagging), where a few dolphins may do this for short periods or multiple dolphins will snag together.
Socialising	Dolphins in close association with each other, and body contact and rubbing is observed, and may be in association with leaping, head outs, genital displays and rapid swims. Splashing is associated with more intensive socialising. Vocalisation whistles can sometimes be heard from the boat above air and/or with a hydrophone.
Travelling	Dolphins swim in a constant and regular direction. Dolphins may travel with short, consistent inter-breath intervals and do shallow dives, or they may take longer inter-breath intervals and still travel in the same direction. The pace of travelling varies, and may even be in association with wave-riding (where the dolphins ride the swell in the gulf).
Unknown	Where dolphins were sighted fleetingly and the predominant behaviour could not be assessed, or where dolphins were not surfacing regularly enough to assign a behavioural state.

chin-up surfacings and were in close proximity to an adult (Mann and Smuts 1999). Juveniles were ~2/3 the length of an adult and mostly swimming independently from an adult; however, during the short time period and purposes of this study, juveniles were not definitively classed here. During dolphin sightings, photographs of individual dolphin dorsal fins were captured with a digital SLR camera (Nikon D610) and telephoto lens (Sigma 50–500 mm) for photo-identification purposes (Würsig and Würsig 1977). The vessel was positioned beside the group to obtain the best lighting from the sun angle on the dorsal fins, and to allow for parallel surfacings of the dolphins for side-on photographs of the dorsal fins. The left and right sides of the fin were captured when possible. Once all individual dolphins in the group were attempted to be photographed, the vessel was returned to the transect line where the group was first sighted and survey effort was resumed.

Data processing and analyses

Within each dolphin sighting, photographs of dolphin dorsal fins were examined and individuals were identified (Würsig and Würsig 1977). Only good and excellent-quality photographs according to focus and contrast, relative angle to the fin, and the size of dorsal fin relative to the frame were used to identify individuals (Urian *et al.* 2015). Nicks and notches on the dolphin's dorsal fin, and secondary markings (such as tooth rake marks and failed predation attempts from sharks), which generally fade over time, were used as an aid for matching individuals. Dolphins with clean fins (no distinctive nicks or notches) were not used for photo-identification, as they could not be individually recognised, and were marked as 'unknown' individuals. The proportion of marked dolphins in the region is high, being 0.80 for bottlenose dolphins and 0.83 for humpback dolphins (Hunt *et al.* 2017; Haughey *et al.* 2020). Individual dorsal fins were compared to existing dolphin dorsal fin photo-identification catalogues developed for the North West Cape on humpback dolphins (Hunt *et al.* 2020) and bottlenose dolphins (Haughey *et al.* 2021). Any new dolphins that were not found in the North West Cape catalogue by three researchers were classed as 'new' dolphins and added to the Exmouth Gulf photo-identification catalogue with a new individual number.

Once individuals within a group were photo-identified, the group size was confirmed with the best estimate from the field and confirmed. Calculations were then made on the average group size, group encounter rate (number of dolphin groups sighted on-effort per kilometre surveyed), individual encounter rate (number of individuals sighted on-effort per kilometre surveyed [calculated from the best estimate of all dolphins]), the total number of individually marked dolphins, the total number of dolphins matched to the North West Cape catalogue, the number of resightings of individuals and the number of females with dependent calves. The spatial coverage of dolphins sighted was assessed using a

density analysis. The kernel density tool was used in the spatial analyst toolbox in Esri's ArcGIS® 10.8 (Esri, Redlands, California). Density distributions were calculated on the basis of the number of dolphin groups sighted and the number of individuals sighted within groups while on-effort. Input provided was a 1000 m radius in 200 m × 200 m cell size, following Smith *et al.* (2016) and Sprogis *et al.* (2018a). For display purposes, the density symbology was stretched, showing the minimum and maximum density, with higher density areas used by dolphin groups indicated by darker coloured clusters. The interpolation with barriers tool was not required at this fine scale because the parallel coastline did not obstruct the analysis (Sprogis *et al.* 2016). The Universal Transverse Mercator projection Zone 50 South (114–120°E) based on the WGS 1984 datum was used.

Results

Survey effort

Surveys were conducted over 32 days between 17 May and 26 July 2021, in daylight hours from 07:00 hours to 18:00 hours, depending on weather conditions. A total of 181 h was spent on the water, covering 1961.7 km. Time on-effort consisted of 113 h and covered 809.35 km. In total, seven replicates of the transects (complete surveys of the study area) were completed during the study period (Fig. 2).

Bottlenose dolphin sightings

There were 93 sightings (62 on-effort, 31 off-effort) of bottlenose dolphin groups, with an encounter rate of 0.077 groups/km or 0.439 individuals/km (Table 2). Core areas of use for bottlenose dolphin groups were along the stretch of coast from Mowbowra Creek to Shothole Creek, (Fig. 3). The largest dolphin group comprised 26 dolphins, and was located north-east of the marina (Fig. 3, Table 2). Bottlenose dolphins were sighted above benthic habitat types of reef, seagrass, macroalgae and sand. Bottlenose dolphins were sighted on-effort mainly travelling (44%, 27/62), followed by foraging (24%, 15/62), socialising (15%, 27/62), milling (11%, 7/62) and resting (5%, 3/62; Figs 3a, 4a). Dolphins were observed feeding on fish in several locations, including the Exmouth Marina entrance, and at the Exmouth marina boat ramp. Dolphins were sighted feeding on squid on one occasion, where two dolphins captured prey on the surface and a large amount of black ink dispersed (squid was the assumed prey rather than cuttlefish as no cuttle bone was observed floating to the surface). When prey was visible, bottlenose dolphins were observed feeding on mullet (*Mugilidae*), long tom (*Belonidae* including barred longtom, *Ablennes hians*), and garfish (*Hemiramphus robustus*).

In total, 199 unique individually marked bottlenose dolphins were identified (excluding clean fins and calves;

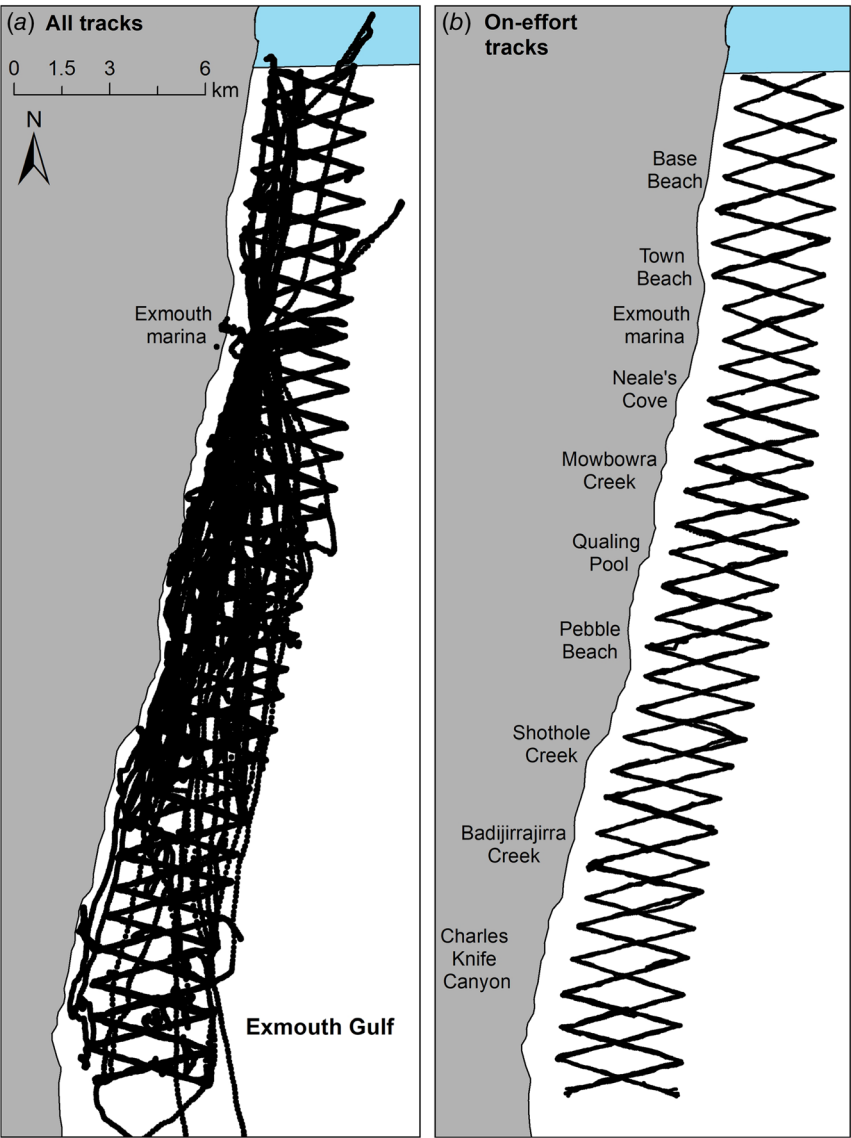


Fig. 2. Map of the study area displaying the survey effort of (a) all boating tracks, including transit routes to and from the Exmouth Marina, and (b) the on-effort tracks while scanning for animals following the pre-determined zig-zag line transects.

Table 2. The number of dolphin groups sighted (on-effort, off-effort), encounter rate (on-effort groups/on-effort survey km and number of individuals in group sightings/on-effort survey km), and range (mean ± s.d.) of group sizes, water depths and water temperatures at which dolphins were observed.

Species	Sightings	Encounter rate (groups/km)	Encounter rate (ind./km)	Group size	Water depth (m)	Water temperature (°C)	Turbidity (m)
Bottlenose dolphins	93 (62, 31)	0.077 (62/809.35)	0.439 (355/809.35)	1–26 (5.3 ± 4.6)	2.3–18.2 (10.8 ± 3.96)	17.8–25 (21.3 ± 2.1)	0.5–16 (6.2 ± 2.73)
Humpback dolphins	15 (12, 3)	0.015 (12/809.35)	0.077 (62/809.35)	1–23 (4.1 ± 5.6)	4.5–15 (10.3 ± 3.22)	19–24.7 (21.5 ± 2.14)	3–9.7 (5.5 ± 1.97)
Interspecific	6 (4,2)	0.005 (4/809.35)	0.082 (66/809.35)	4–39 (13.0 ± 13.2)	4.2–12.1 (7.75 ± 3.13)	18.8–23.8 (20.5 ± 1.83)	2–7.5 (4.67 ± 2.26)

Fig. 5). Of these dolphins, 90 were previously identified in the North West Cape catalogue, and 109 were new dolphins to the catalogue. These dolphins (adults/juveniles) were resighted from one to nine times (mean ± s.d., 2.2 ± 1.75), with half

sighted only once (99/199 dolphins). There were 30 calves identified that were dependent on their mother (14 identified with adults from the North West Cape catalogue). Of these calves, three were newborns, which were dark in appearance

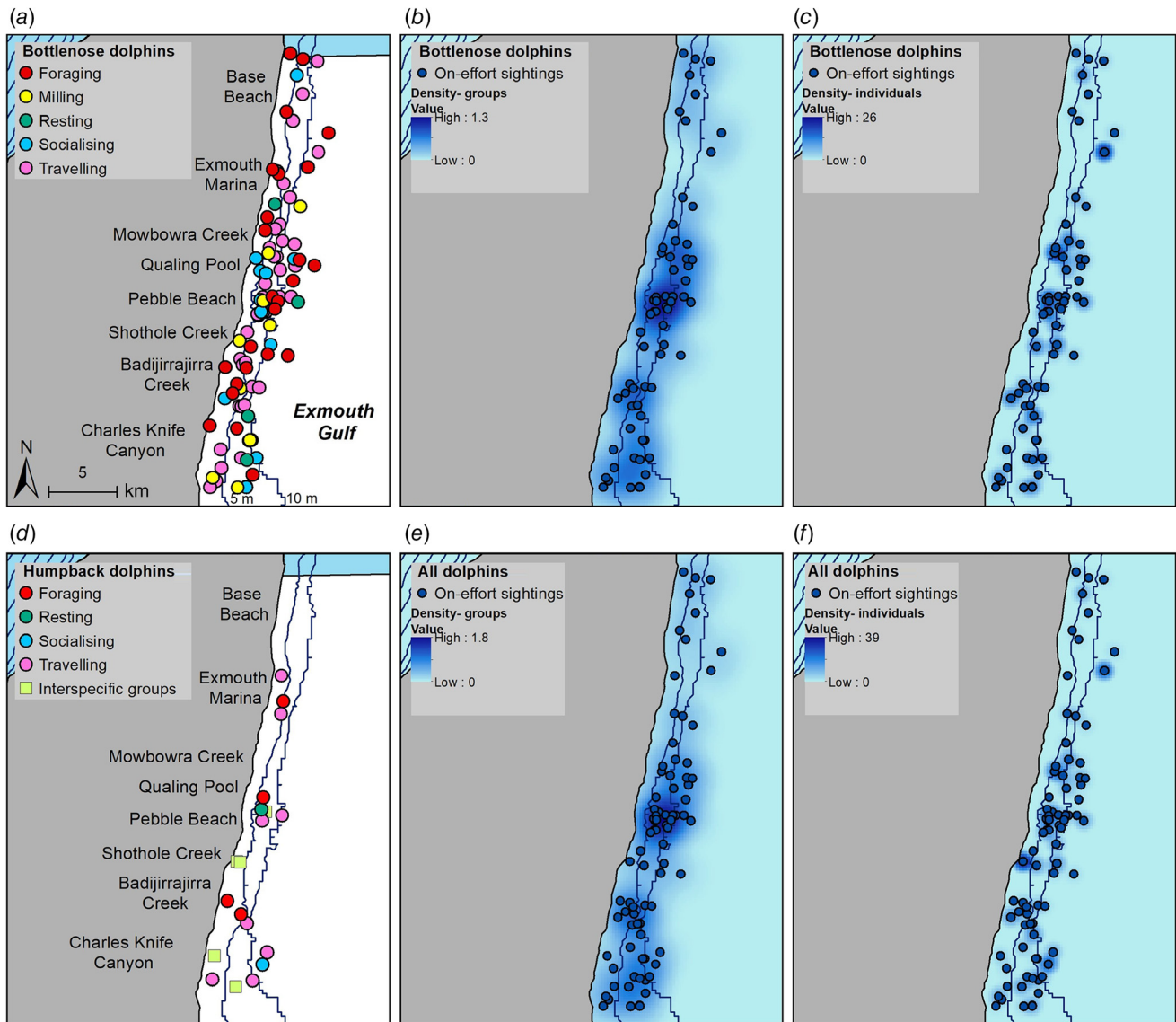


Fig. 3. Spatial distribution of dolphin groups sighted in the study area, displaying (a) bottlenose dolphin groups sighted (on- and off-effort) that were foraging, milling, resting, socialising and travelling (group size 1–26 dolphins), (b) density distribution of bottlenose dolphins with the density based on the number of groups sighted (on-effort, $n = 62$), (c) density distribution of bottlenose dolphins with the density based on the number of individuals within a group (on-effort), (d) humpback dolphin and interspecific groups (humpback dolphin and bottlenose dolphin) sighted (on- and off-effort) that were foraging, resting, socialising and travelling (group size 1–39 dolphins), (e) density distribution of all dolphins (humpback dolphin, bottlenose dolphin and interspecific groups), with the density based on the number of groups sighted (on-effort, $n = 80$), (f) density distribution of all dolphins (humpback dolphin, bottlenose dolphin and interspecific groups), with the density based on the number of individuals within a group. The darker clustered areas represent a higher density.

(Fig. 6a), and were first sighted in late May, mid-June and late June. Fresh failed predation attempts from sharks were present on two bottlenose dolphins (Fig. 6b). On the 26 May, a deceased dolphin washed ashore on Base Beach, this calf was sighted twice during May in baby position next to its mother. The length of the calf was 140 cm from the rostrum to the notch of the tail, suggesting that the calf could be around two years of age (van Aswegen *et al.* 2019). The mother was sighted again in July with no calf, with new nicks and a sliced off dorsal fin that was already healing.

Humpback dolphin sightings

There were 15 sightings (12 on-effort, three off-effort) of humpback dolphin groups, with an encounter rate of 0.015 groups/km or 0.077 individuals/km (Table 2). Core areas of use for humpback dolphin groups were between Qualing Pool and Pebble Beach, and around Badjirrajirra Creek (no separate density distribution presented as minimal sightings, Fig. 3). The largest group of humpback dolphins comprised 23 dolphins sighted socialising off Charles Knife

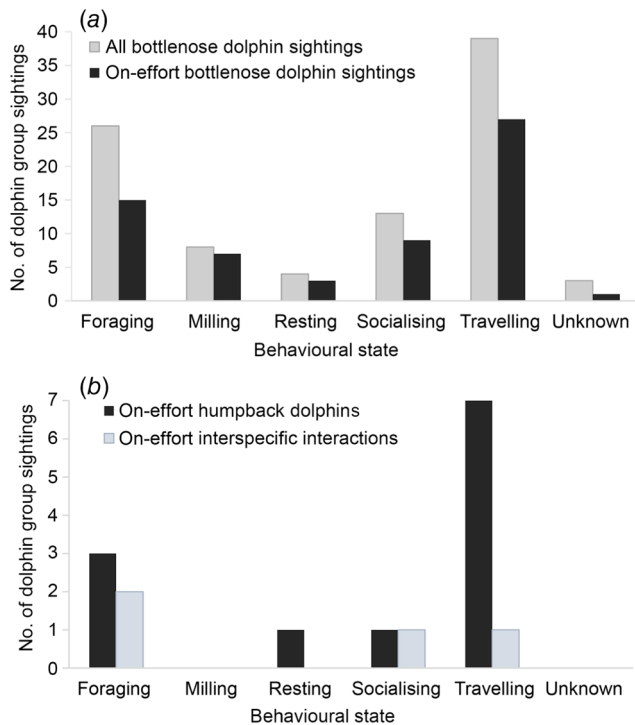


Fig. 4. Frequency distribution of (a) the number of on-effort ($n = 62$) and on- and off-effort ($n = 93$) bottlenose dolphin groups observed foraging, milling, resting, socialising, travelling or unknown behaviour, and (b) the number of on-effort humpback dolphin groups ($n = 12$) and interspecific groups ($n = 4$) observed foraging, resting, socialising and travelling.

Canyon (Fig. 3, Table 2). Humpback dolphins were sighted above reef and mixed habitat types. Humpback dolphins were sighted on-effort primarily travelling (58%, 8/12), followed by foraging (25%, 3/12), resting (8%, 1/12) and socialising (8%, 1/12) (Figs 3, 7). Off-effort sightings consisted of foraging ($n = 2$) and travelling ($n = 1$) dolphins. Humpback

dolphins were not directly observed feeding on prey, therefore prey species could not be identified.

A total of 48 unique individually marked humpback dolphins were identified (excluding clean fins and calves; Fig. 5). Fourteen humpback dolphins were identified in the North West Cape identification catalogue, and 34 were new dolphins to the catalogue. Individuals were resighted on one to three occasions (mean $\pm$ s.d., 1.6 ± 0.74), with 63% being sighted only once (30/48 dolphins). From all humpback dolphins photo-identified (incl. those in interspecific groups), there were four calves dependent on their lactating mothers. Of these calves, two were classed as newborns and were dark on the cape and light elsewhere, and were first sighted late June and mid-July (Fig. 6c).

Interspecific groups (bottlenose dolphins and humpback dolphins)

Bottlenose dolphins and humpback dolphins were observed together within the same group on six occasions (four on-effort, two off-effort), representing 5% of all on-effort dolphin sightings (4/78; Fig. 3; Table 2). The encounter rate was 0.005 groups/km or 0.082 individuals/km (Table 2). Interspecific groups occurred in shallow waters from Pebble Beach to Charles Knife Canyon (Fig. 3d). Groups were sighted over several benthic habitat types, including reef, sponges, sargassum and sand. The group size ranged from 4–39 (mean 13.0 ± 13.2 s.d.), with the largest group sighted off Shothole Creek (Fig. 3f, Table 2). Groups were composed of 2–34 bottlenose dolphins (mean $\pm$ s.d., 9.7 ± 12.3) and two to five humpback dolphins (3.3 ± 1.2). Interspecific groups were sighted travelling (50%, 3/6), foraging (33%, 2/6), and socialising (17%, 1/6) (Fig. 4b). While foraging, bottlenose dolphins were chasing gar fish, snacking on their backs, porpoising at speed, and tail diving, whereas humpback dolphins were not observed exhibiting these behaviours.

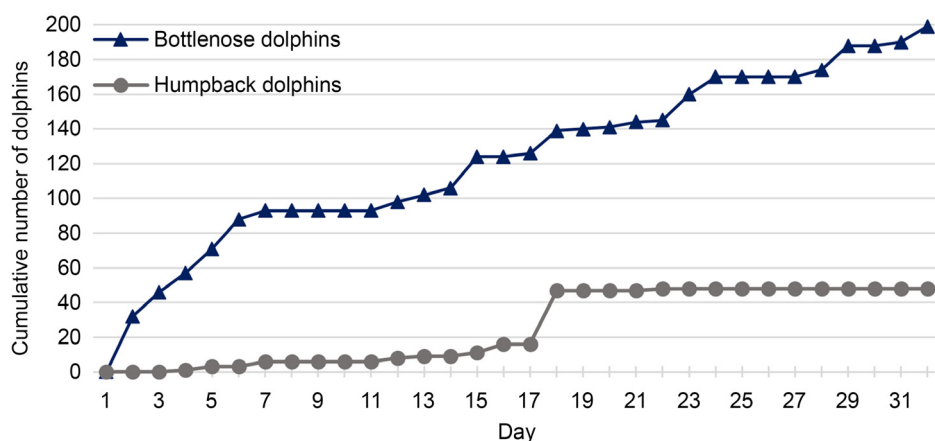


Fig. 5. Cumulative discovery curve of the number of adult and juvenile bottlenose and humpback dolphins photo-identified (excluding clean fins and calves) over 32 days (on- and off-effort sightings) between 17 May and 26 July 2021.



Fig. 6. Representative photographs of (a) a newborn bottlenose dolphin in close proximity next to its mother, with fetal folds (vertical stripes) visible along the body from being compacted *in utero*, and (b) adult bottlenose dolphin with a shark bite from an unidentified shark species, where the arc shape of the injury is representative of an interaction with a shark (Smith *et al.* 2018; Sprogis *et al.* 2018b), (c) a newborn humpback dolphin with dark cape in appearance and popping out of the water when surfacing, and (d) a socialising interspecific group of bottlenose dolphins and humpback dolphins, where the humpback dolphins would continually raise their heads out of the water (note: the dorsal fin is a bottlenose dolphin fin). Dorsal fins show examples of marked bottlenose dolphins, with nicks and notches used to identify individual dolphins.

While socialising, there was physical contact between species (with tight group cohesiveness) resulting in fresh wounds (red blood) on humpback dolphin dorsal fins. Humpback dolphins were observed leaping out of the water and often raising their head out of the water (Fig. 6d).

Other marine megafauna of interest

A range of marine megafauna were observed during the study period, including humpback whales, southern right whales, dugongs, turtles, sea snakes, manta rays and sharks (Table 3). Humpback whales were sighted from the 11 June onward (Table 3), with an increase in sightings in July (June = three sightings, July = 29 sightings). Sightings of groups were recorded throughout the study area (Fig. 7a), travelling (south $n = 2$, north $n = 7$), resting ($n = 2$), displaying surface active behaviours ($n = 7$), and unknown behaviour ($n = 14$). Whales were classed as subadults and adults, with no young of year calves sighted (age classes were not assigned to individuals, because often whales were sighted fleetingly). A southern right whale mother–calf pair (young-of-year) was sighted on transect on the 26 July, and was travelling north through the Exmouth marina boating channel (Table 2, Fig. 7a). Dugongs were sighted across the study period, with mother–calf pairs sighted on six

occasions (Table 3). Dugongs were recorded over reef/seagrass/algal areas, with frequent sightings off the rock platform (Squid Rock) north of Qualing pool and south of the marina channel (Neale's Cove; Fig. 7a). Turtles were sighted over the study period, as individuals and, on two occasions, with two turtles close to each other (Table 3). Turtles were found across reef/seagrass areas and in areas similar to those of dugongs (Fig. 7b). Sightings of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles (unknown number of each species) were confirmed. Sea snakes were observed across the study period, and commonly around Exmouth marina (Fig. 7c). The species identified were the olive sea snake (*Aipysurus laevis laevis*), olive-headed sea snake (*Hydrophis major*) and Dubois' sea snake (*Aipysurus duboisii*; unknown number of each species). Manta rays were sighted in June and July, commonly above reef located off Town Beach and Base Beach (Fig. 7d). Manta rays were sighted filter feeding (mouths open and cephalic lobes unfurled) in the tidelines. Sharks were sighted on two occasions swimming along the surface (Fig. 7d), including (1) a hammerhead shark (*Sphyrna* sp.) sighted 28 May, ~1 m in length, and (2) a zebra shark (*Stegostoma tigrinum*) sighted 17 June, ~1.5 m in length with dark spots.

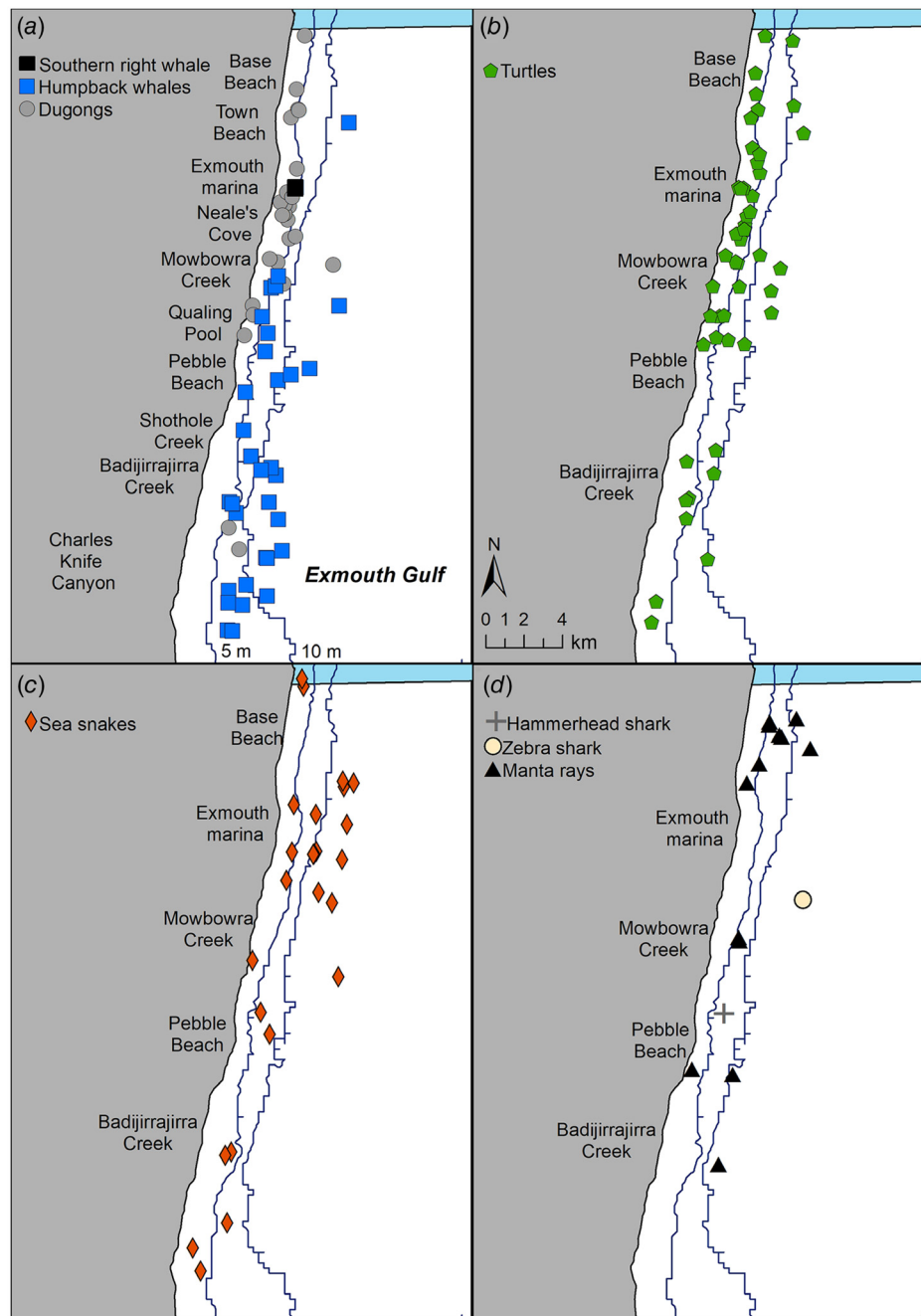


Fig. 7. The distribution of marine megafauna of interest within the study area in Exmouth Gulf from May to July 2021: (a) humpback whales, southern right whales, and dugongs, (b) turtles, (c) sea snakes, and (d) elasmobranchs; manta rays, and hammerhead and zebra sharks.

Discussion

Adequate baseline data on marine fauna is required to effectively assess the potential environmental impact from coastal developments. Here, we present preliminary data on the distribution, encounter rate, group size and behaviour of dolphins and the presence of other marine megafauna off the western coastline of Exmouth Gulf where there is a

current proposal for coastal development. Boat-based surveys over the cooler months indicate that Indo-Pacific bottlenose and Australian humpback dolphins use these coastal waters regularly during this time. The Australian snubfin dolphin was not observed, despite previous records in Exmouth Gulf, albeit limited (e.g. Allen *et al.* 2012; Hanf *et al.* 2022). Snubfin dolphins were also not sighted during dedicated studies in adjacent waters of the North West

Table 3. The number of marine megafauna group sightings, displaying the range (mean $\pm$ s.d.) in group size, water depth and water temperature.

Megafauna	Sightings	Group size	Water depth (m)	Water temperature ($^{\circ}$ C)
Humpback whales	32	1–3 (1.3 $\pm$ 0.60)	5–19.5 (12.4 $\pm$ 3.26)	18.7–21.6 (20.6 $\pm$ 1.01)
Southern right whales	1	2	9.1	22.2
Dugongs	25	1–4 (1.4 $\pm$ 0.81)	3.0–15.8 (7.5 $\pm$ 3.69)	18–24.8 (22 $\pm$ 2.21)
Turtles	54	1–2 (1.04 $\pm$ 0.19)	1.9–17.7 (8.0 $\pm$ 4.06)	17.4–25 (21.0 $\pm$ 2.36)
Sea snakes	27	1	3.0–18.0 (10.6 $\pm$ 5.77)	19–25 (22.2 $\pm$ 1.73)
Manta rays	13	1	4.4–16.0 (11.2 $\pm$ 3.69)	19.4–22.5 (21.7 $\pm$ 0.77)
Sharks (hammerhead)	1	1	11.8	23.4
Sharks (zebra)	1	1	18.2	21.5

Cape (e.g. [Hunt et al. 2020](#); [Haughey et al. 2021](#)). The limited sightings of snubfin dolphins in the north-western gulf suggest that the species may not frequently use these waters and/or that individuals sighted are from the eastern gulf or are vagrants from more northern populations (e.g. [Brown et al. 2016](#)). However, the waters are utilised by a range of marine megafauna, including humpback whales, southern right whales, dugongs, turtles, sea snakes, manta rays and sharks.

Dolphin distribution, encounter rates, group size, behaviour and photo-identification

Dolphins were encountered across the study area, with core areas for bottlenose dolphin groups off Pebble Beach, and humpback dolphin groups off Pebble Beach and around Badijirrajirra Creek (albeit limited sightings; [Fig. 3](#)). Dolphins were sighted in an average water depth of 10 m, ranging from 2.3 to 18.2 m depth for bottlenose dolphins and 4.5–15 m depth for humpback dolphins ([Table 2](#)). Around the North West Cape, water depth is a driver of bottlenose and humpback dolphin distribution, with dolphins also preferring shallow waters of <15 m deep ([Hunt et al. 2020](#); [Haughey et al. 2021](#)). Elsewhere in Australia, water depth also has a strong influence on dolphin habitat use, with a decrease in sightings with increasing depth ([Meager et al. 2018](#); [Sprogis et al. 2018a](#)). The home range size of individual dolphins residing within the gulf study area (150 km²) is yet to be determined, and could be assessed with a greater number of re-sightings. On the basis of research on the home range size of individual coastal dolphins ([Hung and Jefferson 2004](#); [Passadore et al. 2018](#)), resident individuals may show small ranging patterns, with males ranging further than females ([Sprogis et al. 2016](#)).

The dolphin species most frequently observed at this time of the year (autumn/winter) was the bottlenose dolphin, with an encounter rate of 0.08 groups/km, compared with 0.02 groups/km for humpback dolphins. Off the North West Cape, also during the cooler months, the encounter rate of bottlenose dolphins was 0.05 groups/km (182 groups/3450 km surveyed; [Haughey et al. 2020](#)), and of humpback dolphins it was 0.04 groups/km (145 groups/3450 km

surveyed; [Hunt et al. 2017](#)). The encounter rate of humpback dolphins around the North West Cape represents a particularly high density for this species ([Hunt et al. 2017](#)). In the gulf, dolphins were observed in small group sizes, with average group sizes of 5.3 ($\pm$ 4.6 s.d.) bottlenose dolphins and 4.1 ($\pm$ 5.6) humpback dolphins. These group sizes are comparable to the group sizes recorded around the North West Cape (mean $\pm$ s.d., 6.4 $\pm$ 5.2 bottlenose dolphins, and 4.6 $\pm$ 3.2 humpback dolphins; [Hunt et al. 2017](#); [Haughey et al. 2020](#)), and other locations in WA (mean 3.0 humpback dolphins, [Raudino et al. 2018](#); mean 5.98 bottlenose dolphins, [Sprogis et al. 2016](#)).

Dolphins were commonly observed travelling and foraging. Bottlenose dolphins were photographed feeding on mullet (*Mugilidae*), robust garfish (*H. robustus*) and long tom (*Belonidae*). There is a diversity of fishes in Exmouth Gulf that could represent potential dolphin prey, including trevally (*Carangidae*), emperor (*Lutjanidae*), snapper (*Sparidae*), and flathead (*Platycephalidae*) ([Florisson et al. 2020](#)). The full expanse of the diet of bottlenose dolphins in Exmouth Gulf remains unknown; however, it may be similar to the diet of Indo-Pacific bottlenose dolphins elsewhere in WA, which includes octopus ([Sprogis et al. 2017](#)), cuttlefish ([Smith and Sprogis 2016](#)), and a multitude of fish species ([McCluskey et al. 2021](#); [Nicholson et al. 2021](#)). Humpback dolphins were not directly observed catching or chasing fish; therefore, it remains unknown as to what kind of prey they feed on in Exmouth Gulf. Stomach content studies suggest that Australian humpback dolphins are opportunistic-generalist feeders, preying on a wide variety of fish and cephalopods that are readily available in shallow coastal-estuarine environments ([Parra and Jedensjö 2014](#)). Humpback dolphins were commonly sighted near freshwater runoff areas (e.g. Qualing Pool and Badijirrajirra Creek), suggesting that the mixing of water salinities may be of importance. This is in alignment with [Hanf et al. \(2022\)](#), showing that shallow intertidal areas are important areas for humpback dolphins, as they are for this species elsewhere in Australia ([Parra 2006](#); [Meager et al. 2018](#)).

There were 199 individual bottlenose and 48 humpback dolphins photo-identified along the western coastline of the gulf from May to July. This number of individuals is expected to grow with a greater temporal and spatial coverage. Even so, within this timeframe, individual bottlenose dolphins were resighted up to nine times (mean $\pm$ s.d., 2.2 ± 1.75). Humpback dolphin individuals were resighted to a lesser extent (1.5 ± 0.74) compared with bottlenose dolphins. Further data collection, across different seasons, is required to understand any temporal patterns (i.e. Sprogis and Waddell 2022). Around the North West Cape, from effort over three seasons and across multiple years, humpback dolphins were resighted on average on four occasions (± 3.0 s.d.), representing a high density (Hunt *et al.* 2017). Of the bottlenose and humpback dolphins photo-identified along the western coastline, a minimum of 90 bottlenose and 14 humpback dolphins were previously sighted around the North West Cape (Hunt *et al.* 2020; Haughey *et al.* 2021). These sightings of individuals across both areas are considered a minimum estimate of individuals as the North West Cape photo-identification catalogue was last updated in September 2019 and dorsal fins are likely to have received new nicks and notches in that time (mark evolution; Urian *et al.* 2015). Despite this, resightings corroborate previous studies in the North West Cape, suggesting that the home ranges of dolphins extend into the inner waters of Exmouth Gulf (Hunt *et al.* 2020; Haughey *et al.* 2021), and highlight the interconnectedness between Exmouth Gulf and the UNESCO Ningaloo Coast World Heritage Area.

There were 30 bottlenose dolphin calves (including three newborns) and four humpback dolphin calves (including two newborns) observed. The approximate birth of newborns in autumn and winter contribute to the knowledge on calving in this tropical region ($21^{\circ}57'S$). In more southerly latitudes of WA, bottlenose dolphins display moderate seasonality in calving, peaking from October to December (spring/summer) in Shark Bay ($25^{\circ}47'S$), and from December to March (summer/autumn) off Bunbury ($33^{\circ}32'S$; Mann *et al.* 2000; Smith *et al.* 2016). Off Bunbury, across a 3-year period, only six newborn bottlenose dolphins were born over the cooler months (May–August), emphasising the summer/autumn calving season in warmer waters ($n = 30$ newborns; Smith *et al.* 2016). Off Bunbury and Shark Bay, calving peaked when the water temperature was above $20^{\circ}C$ (Mann *et al.* 2000; Smith *et al.* 2016). Calving in Exmouth Gulf may not be as seasonally defined as in these southerly locations, especially considering that the average water temperature during dolphin sightings in the gulf was 21 – $22^{\circ}C$ during the cooler months (late autumn/winter). This is similar to the north-east of Exmouth Gulf, off Onslow ($21^{\circ}38'S$), where humpback dolphin newborns were also observed over the cooler months (Raudino *et al.* 2018). A dedicated study is required to examine calving rates across the year in Exmouth Gulf. However, the recorded number of calves and newborns highlights the importance of gulf

waters for lactating mothers and their calves and that the habitat used may provide critical resources for calf development and survival (i.e. availability of suitable prey, and protected habitats; Fury *et al.* 2013; Sprogis *et al.* 2018a).

Interspecific groups (bottlenose dolphins and humpback dolphins)

Bottlenose dolphins and humpback dolphins are sympatric species and have overlapping ranges and habitats around the North West Cape (Hunt *et al.* 2020; Haughey *et al.* 2021), and are recorded in Exmouth Gulf (Brown *et al.* 2012; de Freitas *et al.* 2015). Interspecific groups were observed associating in the gulf (0.005 groups/km), with close interactions while socialising. The average group size of interspecific interactions in the gulf was 13 dolphins (± 5.38 s.e.), which is comparable to those observed around the North West Cape (9.5 ± 1.33 s.e.; Brown *et al.* 2012). Groups in Exmouth Gulf, observed from May–July, were composed of a greater number of bottlenose dolphins than humpback dolphins (average of 9.7 ± 5.02 – 3.3 ± 0.56 s.e. respectively), whereas around the North West Cape, with data collected in April 2010, there were fewer bottlenose dolphins than humpback dolphins (average 4.2 ± 0.66 – 5.5 ± 0.96 s.e. respectively; Brown *et al.* 2012). Numerous species of delphinids have been observed in interspecific associations elsewhere, including bottlenose and humpback dolphins (Stensland *et al.* 2003; Syme *et al.* 2021), including off the east coast of Australia (Corkeron 1990). *Tursiops* spp. and *Sousa* spp. have also been recorded to associate elsewhere (Stensland *et al.* 1998), where there are reports of aggressive social behaviours off South Africa (Saayman *et al.* 1972), Madagascar (Cerchio *et al.* 2015), and the Arabian coast (Baldwin *et al.* 2004). Future studies are required to understand the functional significance of interspecific groups, and determine whether the groups observed in Exmouth Gulf and North West Cape represent aggregations (i.e. co-occurring species attracted to a common resource or that respond in a similar way to environmental stimuli), chance encounters (i.e. that result from the coincidental meeting of co-occurring species) and/or mixed-species groups (i.e. individuals of two or more species found in close spatial proximity because of mutual or unreciprocated attraction derived from evolutionary grouping benefits) (Syme *et al.* 2021).

Other marine megafauna in Exmouth Gulf

The sightings of at least 12 other marine megafauna species displaying critical behaviours such as resting, socialising, feeding and presumed nursing indicate the gulf as an area of high importance for a variety of marine life. For humpback whales, the gulf is already recognised as an important resting and nursing area (Chittleborough 1953; Jenner and Jenner 2005; Bejder *et al.* 2019; Ejrnæs and Sprogis 2022), and

here we documented whales from June onward coinciding with their northerly migration. A southern right whale mother–calf pair was observed, with this region being the most northerly distribution recorded for southern right whales in WA (Allen and Bejder 2003), further emphasising the use of the gulf by this endangered species (EPBC Act 1999). Dugongs and turtles were commonly sighted in similar areas over shallow reef, seagrass and algal patches (such as at Neale's Cove and north of Qualing Pool), which is likely to be due to shared seagrass food resources (e.g. for green turtles and dugongs; Preen 1995; Vanderklift *et al.* 2021). Dugongs, listed as vulnerable (Marsh and Sobtzick 2019), were mainly sighted as singles or mother–calf pairs. Green (*C. mydas*) and loggerhead (*C. caretta*) turtles were sighted; however, flatback (*Natator depressus*) and hawksbill (*Erectmochelys imbricata*) turtles are also documented in the gulf, although not confirmed during this study. Sea snakes were sighted swimming along the surface, predominantly in the shallow waters off Exmouth marina. Numerous species of sea snake can be sighted in Exmouth Gulf ($n = \sim 15$; Fitzpatrick *et al.* 2019). The sea snake species identified here were the olive sea snake (*A. laevis laevis*), olive-headed sea snake (*H. major*) and Dubois' sea snake (*A. duboisii*); however, other species were not confirmed, such as the critically endangered short-nosed sea snake (*Aipysurus apraefrontalis*; D'Anastasi *et al.* 2016). Manta rays, listed as vulnerable to extinction (Marshall *et al.* 2019), were sighted feeding in shallow waters above reef, or in the tidelines. Manta rays move throughout the southern gulf (Armstrong *et al.* 2020), and, in the present study, were mostly sighted around Base Beach. Sharks were the least sighted of the species, which is not unexpected, given they do not need to surface to breathe. Several species of shark are found in the gulf (e.g. tiger and reef sharks; Fitzpatrick *et al.* 2019; Sutton and Shaw 2021); however, during this study, a hammerhead shark and zebra shark were sighted on the surface. The small size (<1.5 m length) and colouration (i.e. zebra shark with pale yellow horizontal stripes; Dudgeon and White 2012) of these sharks and individuals recorded previously in the gulf (K. R. Sprogis, pers. obs.) signify the use of these waters by young sharks, which is of interest for these endangered species (Dudgeon *et al.* 2019; Rigby *et al.* 2019a, 2019b). Detailed boat-based observations of marine megafauna have been lacking in the gulf, and this study documented the use of inshore, shallow waters by these species in an area under particular pressure from development.

Implications for wildlife management

Exmouth Gulf represents an important habitat for threatened and near threatened dolphin species, and a variety of other endangered, vulnerable or threatened marine megafauna. These waters are still currently unprotected; however, they are of high importance to the UNESCO Ningaloo

Coast World Heritage area because these waters are interconnected. In December 2021, after the data collection of this study, it was announced by the Government of Western Australia that a section of the eastern gulf will be designated as a marine park, and the area around Qualing Pool (terrestrial and freshwater) will be protected (Government of Western Australia 2021). However, it is unknown as to what extent the protection around Qualing Pool will include (e.g. if marine waters will be protected). The data presented here provide information on the ecology of marine megafauna species, which is applicable for marine spatial planning and management, and conservation efforts in line with the desire of the Environmental Protection Authority to protect these waters (EPA 2021). This information is of timely importance and pertinent for management agencies (e.g. Western Australian Department of Biodiversity, Conservation and Attractions; Nganhurra Thanardi Garrbu Aboriginal Corporation) and industries to assess conflicts with current proposed coastal developments and make informed decisions about the conservation and management of these species and their associated habitats. Further research with sufficient effort and long-term datasets are required to address the demographic parameters (abundance and survival), home ranges and habitat use of populations (Symons *et al.* 2018).

References

- Allen SJ, Bejder L (2003) Southern right whale *Eubalaena australis* sightings on the Australian coast and the increasing potential for entanglement. *Pacific Conservation Biology* 9, 228–233. doi:10.1071/PC030228
- Allen SJ, Cagnazzi DD, Hodgson AJ, Loneragan NR, Bejder L (2012) Tropical inshore dolphins of north-western Australia: unknown populations in a rapidly changing region. *Pacific Conservation Biology* 18, 56–63. doi:10.1071/PC120056
- Armstrong AJ, Armstrong AO, McGregor F, Richardson AJ, Bennett MB, Townsend KA, Hays GC, van Keulen M, Smith J, Dudgeon CL (2020) Satellite tagging and photographic identification reveal connectivity between two UNESCO world heritage areas for reef manta rays. *Frontiers in Marine Science* 7, 725. doi:10.3389/fmars.2020.00725
- Baker I, O'Brien J, McHugh K, Berrow S (2017) An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Aquatic Mammals* 43, 594–613. doi:10.1578/AM.43.6.2017.594
- Baldwin RM, Collins M, Van Waerebeek K, Minton G (2004) The Indo-Pacific humpback dolphin of the Arabian region: a status review. *Aquatic Mammals* 30, 111–124. doi:10.1578/AM.30.1.2004.111
- Beasley I, Robertson KM, Arnold P (2005) Description of a new dolphin, the Australian snubfin dolphin *Orcaella heinsohni* sp. n. (Cetacea, Delphinidae). *Marine Mammal Science* 21, 365–400.
- Bejder L, Hodgson AJ, Loneragan NR, Allen SJ (2012) Coastal dolphins in north-western Australia: the need for re-evaluation of species listings and short-comings in the environmental impact assessment process. *Pacific Conservation Biology* 18, 22–25. doi:10.1071/PC120022
- Bejder L, Videsen S, Hermannsen L, Simon M, Hanf DM, Madsen PT (2019) Low energy expenditure and resting behaviour of humpback whale mother–calf pairs highlights conservation importance of sheltered breeding areas. *Scientific Reports* 9, 771. doi:10.1038/s41598-018-36870-7
- Braulik G, Natoli A, Kiszka J, Parra G, Plön S, Smith BD (2019) *Tursiops aduncus*. In 'The IUCN red list of threatened species 2019'. Available at

- <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T41714A50381127.en> [Accessed 2 February 2021]
- Brown A, Bejder L, Cagnazzi D, Parra GJ, Allen SJ (2012) The north west cape, western Australia: a potential hotspot for Indo-Pacific humpback dolphins *Sousa chinensis*? *Pacific Conservation Biology* **18**, 240–246. doi:10.1071/PC120240
- Brown AM, Bejder L, Pollock KH, Allen SJ (2016) Site-specific assessments of the abundance of three inshore dolphin species to inform conservation and management. *Frontiers in Marine Science* **3**, 4. doi:10.3389/fmars.2016.00004
- Brunskill GJ, Orpin AR, Zagorskis I, Woolfe KJ, Ellison J (2001) Geochemistry and particle size of surface sediments of Exmouth Gulf, northwest shelf, Australia. *Continental Shelf Research* **21**, 157–201. doi:10.1016/S0278-4343(00)00076-5
- Cartwright PJ, Fearn PRCS, Branson P, Cuttler MVW, O'Leary M, Browne NK, Lowe RJ (2021) Identifying metocean drivers of turbidity using 18 years of MODIS satellite data: implications for marine ecosystems under climate change. *Remote Sensing* **13**, 3616. doi:10.3390/rs13183616
- Cerchio S, Andrianarivelo N, Andrianantenaina B (2015) Ecology and conservation status of Indian Ocean humpback dolphins (*Sousa plumbea*) in Madagascar. *Advances in Marine Biology* **72**, 163–199. doi:10.1016/bs.amb.2015.09.004
- Chittleborough RG (1953) Aerial observations on the humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. *Marine and Freshwater Research* **4**, 219–226. doi:10.1071/MF9530219
- Corkeron PJ (1990) Aspects of the behavioural ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In 'The bottlenose dolphin'. (Eds S Leatherwood, RR Reeves) pp. 245–265. (Academic Press: San Diego, CA, USA)
- D'Anastasi BR, van Herwerden L, Hobbs JA, Simpfendorfer CA, Lukoschek V (2016) New range and habitat records for threatened Australian sea snakes raise challenges for conservation. *Biological Conservation* **194**, 66–70. doi:10.1016/j.biocon.2015.11.032
- de Freitas M, Jensen FH, Tyne J, Bejder L, Madsen PT (2015) Echolocation parameters of Australian humpback dolphins (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the wild. *The Journal of the Acoustical Society of America* **137**, 3033–3041. doi:10.1121/1.4921277
- Dudgeon CL, White WT (2012) First record of potential Batesian mimicry in an elasmobranch: juvenile zebra sharks mimic banded sea snakes? *Marine and Freshwater Research* **63**, 545–551. doi:10.1071/MF11211
- Dudgeon C, Simpfendorfer C, Pillans R (2019) *Stegostoma fasciatum* (amended version of 2016 assessment). In 'The IUCN red list of threatened species 2019: e.T41878A161303882'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T41878A161303882.en> [Accessed 25 November 2021]
- Ejrnæs DD, Sprogis KR (2022) Ontogenetic changes in energy expenditure and resting behaviour of humpback whale mother–calf pairs examined using unmanned aerial vehicles. *Wildlife Research* **49**, 34–45. doi:10.1071/WR20186
- EPA (2021) Potential cumulative impacts of proposed activities and developments on the environmental, social and cultural values of Exmouth Gulf in accordance with section 16(e) of the Environmental Protection Act 1986. (Environmental Protection Authority: WA, Australia)
- EPBC Act (1999) Australian whale sanctuary. In 'Environment Protection and Biodiversity Conservation Act'. (Australian Government, Department of Agriculture, Water and the Environment: Canberra, ACT, Australia)
- Fitzpatrick B, Davenport A, Penrose H, Hart C, Gardner S, Morgan A, Twigg E, Gillis R, Fennell B, D'Anastasi B, Willems A, Dickie J, Taylor M, Armstrong A, Wueringer B, Langlois T (2019) Exmouth Gulf, north western Australia: a review of environmental and economic values and baseline survey of the south western region. (Oceanwise). Report to Jock Clough Marine Foundation. p. 192.
- Florisson JH, Rowland AJ, Harvey ES, Allen MB, Watts SL, Saunders BJ (2020) King Reef: an Australian first in repurposing oil and gas infrastructure to benefit regional communities. *The APPEA Journal* **60**, 435–439. doi:10.1071/AJ19134
- Fury CA, Ruckstuhl KE, Harrison PL (2013) Spatial and social sexual segregation patterns in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *PLoS ONE* **8**, e52987. doi:10.1371/journal.pone.0052987
- Government of Western Australia (2021) Historic protections to safeguard spectacular Exmouth Gulf. In 'Media statements.' (Government of Western Australia: Perth, WA, Australia) Available at www.mediastatements.wa.gov.au/Pages/McGowan/2021/12/Historic-protections-to-safeguard-spectacular-Exmouth-Gulf.aspx [Accessed 3 December 2021]
- Hanf DM, Hunt T, Parra GJ (2016) Humpback dolphins of Western Australia: a review of current knowledge and recommendations for future management. *Advances in Marine Biology* **73**, 193–218.
- Hanf DM, Hodgson AJ, Kobryn HT, Bejder L, Smith JN (2022) Dolphin distribution and habitat suitability in north western Australia: applications and implications of a broad-scale, non-targeted dataset. *Frontiers in Marine Science* **8**, 733841. doi:10.3389/fmars.2021.733841
- Haughey R (2021) Population demographics and spatial ecology of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting coastal waters at the North West Cape, Western Australia. PhD thesis. Flinders University, Adelaide, SA, Australia.
- Haughey R, Hunt T, Hanf D, Rankin RW, Parra GJ (2020) Photographic capture–recapture analysis reveals a large population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) with low site fidelity off the north west cape, western Australia. *Frontiers in Marine Science* **6**, 781. doi:10.3389/fmars.2019.00781
- Haughey R, Hunt TN, Hanf D, Passadore C, Baring R, Parra GJ (2021) Distribution and habitat preferences of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting coastal waters with mixed levels of protection. *Frontiers in Marine Science* **8**, 617518. doi:10.3389/fmars.2021.617518
- Hodgson A (2007) The distribution, abundance and conservation of dugongs and other marine megafauna in Shark Bay Marine Park, Ningaloo Reef Marine Park and Exmouth Gulf. Report to the Western Australia Department of Environment and Conservation. p. 34.
- Hung SK, Jefferson TA (2004) Ranging patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the pearl river Estuary, People's Republic of China. *Aquatic Mammals* **30**, 159–174. doi:10.1578/AM.30.1.2004.159
- Hunt T (2018) Demography, habitat use and social structure of Australian humpback dolphins (*Sousa sahulensis*) around the North West Cape, Western Australia: implications for conservation and management. PhD thesis, Flinders University, Adelaide, SA, Australia.
- Hunt TN, Bejder L, Allen SJ, Rankin RW, Hanf D, Parra GJ (2017) Demographic characteristics of Australian humpback dolphins reveal important habitat toward the southwestern limit of their range. *Endangered Species Research* **32**, 71–88. doi:10.3354/esr00784
- Hunt TN, Allen SJ, Bejder L, Parra GJ (2019) Assortative interactions revealed in a fission–fusion society of Australian humpback dolphins. *Behavioral Ecology* **30**, 914–927. doi:10.1093/beheco/arz029
- Hunt TN, Allen SJ, Bejder L, Parra GJ (2020) Identifying priority habitat for conservation and management of Australian humpback dolphins within a marine protected area. *Scientific Reports* **10**, 14366. doi:10.1038/s41598-020-69863-6
- Irvine AB, Scott MD, Wells RS, Kaufmann JH (1981) Movements and activities of the Atlantic bottlenose dolphin (*Tursiops truncatus*) near Sarasota Florida USA. *Fishery Bulletin (Washington DC)* **79**, 671–688.
- Irvine L, Salgado Kent C (2019) The distribution and relative abundance of marine mega-fauna, with a focus on humpback whales (*Megaptera novaeangliae*), in Exmouth Gulf, western Australia, 2018. Report prepared for Subsea 7. Attachment 2J Humpback Whale Aerial Survey Report. (Exmouth: Western Australia) p. 25.
- Jefferson TA, Rosenbaum HC (2014) Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. *Marine Mammal Science* **30**, 1494–1541. doi:10.1111/mms.12152
- Jenner KCS, Jenner MN (2005) Distribution and abundance of humpback whales and other mega-fauna in Exmouth Gulf, Western Australia, during 2004/2005. (Straits Salt: Fremantle, WA) p. 24.
- Lebrech U, Paumard V, O'Leary MJ, Lang SC (2021) Towards a regional high-resolution bathymetry of the north west shelf of Australia based on Sentinel-2 satellite images, 3D seismic surveys, and historical datasets. *Earth System Science Data* **13**, 5191–5212. doi:10.5194/essd-13-5191-2021

- Loneragan NR, Kangas M, Haywood MDE, Kenyon RA, Caputi N, Sporer E (2013) Impact of cyclones and aquatic macrophytes on recruitment and landings of tiger prawns *Penaeus esculentus* in Exmouth Gulf, Western Australia. *Estuarine, Coastal and Shelf Science* **127**, 46–58. doi:10.1016/j.ecss.2013.03.024
- Lyne V, Fuller M, Last P, Butler A, Martin M, Scott R (2006) 'Ecosystem characterisation of Australia's north west shelf.' Technical report. (CSIRO and Department of Environment: Perth, WA, Australia) p. 73.
- MacLeod CD (2010) Habitat representativeness score (HRS): a novel concept for objectively assessing the suitability of survey coverage for modelling the distribution of marine species. *Journal of the Marine Biological Association of the United Kingdom* **90**, 1269–1277. doi:10.1017/S0025315410000408
- Mann J, Smuts B (1999) Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* **136**, 529–566. doi:10.1163/156853999501469
- Mann J, Connor RC, Barre LM, Heithaus MR (2000) Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology* **11**, 210–219. doi:10.1093/beheco/11.2.210
- Marsh H, Sobotzick S (2019) *Dugong dugon* (amended version of 2015 assessment). In 'The IUCN red list of threatened species 2019: e.T6909A160756767'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T6909A160756767.en> [Accessed 25 November 2021]
- Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis M, Herman K, Jabado R, Liu K, Pacoureaux N (2019) *Mobula alfredi*. In 'The IUCN red list of threatened species 2019: e.T195459A68632178'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en> [Accessed 25 November 2021]
- McCluskey SM, Sprogis KR, London JM, Bejder L, Loneragan NR (2021) Foraging preferences of an apex marine predator revealed through stomach content and stable isotope analyses. *Global Ecology and Conservation* **25**, e01396. doi:10.1016/j.gecco.2020.e01396
- McKinnon AD, Ayukai T (1996) Copepod egg production and food resources in Exmouth Gulf, Western Australia. *Marine and Freshwater Research* **47**, 595–603. doi:10.1071/MF9960595
- Meager JJ, Hawkins ER, Ansmann I, Parra GJ (2018) Long-term trends in habitat use and site fidelity by Australian humpback dolphins *Sousa sahulensis* in a near-urban embayment. *Marine Ecology Progress Series* **603**, 227–242. doi:10.3354/meps12709
- Mendez M, Jefferson TA, Kolokotronis S-O, Krützen M, Parra GJ, Collins T, Minton G, Baldwin R, Berggren P, Särnblad A, Amir OA, Peddemors VM, Karczmarski L, Guissamulo A, Smith B, Sutaria D, Amato G, Rosenbaum HC (2013) Integrating multiple lines of evidence to better understand the evolutionary divergence of humpback dolphins along their entire distribution range: a new dolphin species in Australian waters? *Molecular Ecology* **22**, 5936–5948. doi:10.1111/mec.12535
- Nicholson K, Bejder L, Loneragan NR (2021) Niche partitioning among social clusters of a resident estuarine apex predator. *Behavioral Ecology and Sociobiology* **75**, 160. doi:10.1007/s00265-021-03091-4
- Parra GJ (2006) Resource partitioning in sympatric delphinids: space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. *Journal of Animal Ecology* **75**, 862–874. doi:10.1111/j.1365-2656.2006.01104.x
- Parra GJ, Jedensjö M (2014) Stomach contents of Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*). *Marine Mammal Science* **30**, 1184–1198. doi:10.1111/mms.12088
- Parra GJ, Azuma C, Preen AR, Corkeron PJ, Marsh H (2002) Distribution of irrawaddy dolphins, *Orcaella brevirostris*, in Australian waters. *Raffles Bulletin of Zoology Supplement* **10**, 141–154.
- Parra GJ, Corkeron PJ, Marsh H (2004) The Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), in Australian waters: a summary of current knowledge. *Aquatic Mammals* **30**, 197–206. doi:10.1578/AM.30.1.2004.197
- Parra GJ, Corkeron PJ, Marsh H (2006) Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: implications for conservation. *Biological Conservation* **129**, 167–180. doi:10.1016/j.biocon.2005.10.031
- Parra G, Cagnazzi D, Perrin W, Braulik GT (2017a) *Sousa sahulensis*. In 'The IUCN red list of threatened species 2017: e.T82031667A82031671'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T82031667A82031671.en> [Accessed 2 February 2021]
- Parra G, Cagnazzi D, Perrin WF, Braulik GT (2017b) *Orcaella heinsohni* (errata version published in 2018). In 'The IUCN red list of threatened species 2017: e.T82031667A82031671'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T82031667A82031671.en> [Accessed 2 February 2021]
- Passadore C, Möller L, Diaz-Aguirre F, Parra GJ (2018) High site fidelity and restricted ranging patterns in southern Australian bottlenose dolphins. *Ecology and Evolution* **8**, 242–256. doi:10.1002/ece3.3674
- Preen A (1995) Diet of dugongs: are they omnivores? *Journal of Mammalogy* **76**, 163–171. doi:10.2307/1382325
- Preen AR, Marsh H, Lawler IR, Prince RIT, Shepherd R (1997) Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research* **24**, 185–208. doi:10.1071/WR95078
- Raudino HC, Douglas CR, Waples KA (2018) How many dolphins live near a coastal development? *Regional Studies in Marine Science* **19**, 25–32. doi:10.1016/j.rsma.2018.03.004
- Rigby CL, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Marshall A, Pacoureaux N, Romanov E, Sherley RB, Winker H (2019a) *Sphyrna mokarran*. In 'The IUCN red list of threatened species 2019: e.T39386A2920499'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39386A2920499.en> [Accessed 25 November 2021]
- Rigby CL, Dulvy NK, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Marshall A, Pacoureaux N, Romanov E, Sherley RB, Winker H (2019b) *Sphyrna lewini*. In 'The IUCN red list of threatened species 2019: e.T39385A2918526'. Available at <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39385A2918526.en> [Accessed 25 November 2021]
- Saayman GS, Bower D, Tayler CK (1972) Observations on inshore and pelagic dolphins on the southeastern cape of south Africa. *Koedoe* **15**, 1–24. doi:10.4102/koedoe.v15i1.664
- Semeniuk V (1993) The Pilbara coast: a riverine coastal plain in a tropical arid setting, northwestern Australia. *Sedimentary Geology* **83**, 235–256. doi:10.1016/0037-0738(93)90015-W
- Shane SH (1990) Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In 'The bottlenose dolphin'. (Eds S Leatherwood, RR Reeves) pp. 541–558. (Academic Press)
- Smith HC, Sprogis KR (2016) Seasonal feeding on giant cuttlefish (*Sepia apama*) by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in south-western Australia. *Australian Journal of Zoology* **64**, 8–13. doi:10.1071/ZO15075
- Smith HC, Frère C, Kobryn HT, Bejder L (2016) Dolphin sociality, distribution and calving as important behavioural patterns informing management. *Animal Conservation* **19**, 462–471. doi:10.1111/acv.12263
- Smith F, Allen SJ, Bejder L, Brown AM (2018) Shark bite injuries on three inshore dolphin species in tropical northwestern Australia. *Marine Mammal Science* **34**, 87–99. doi:10.1111/mms.12435
- Sprogis KR, Waddell TLR (2022) 'Marine mammal distribution on the western coast of Exmouth Gulf, Western Australia.' Report to the Australian Marine Conservation Society. (Aarhus University and Carijoa Marine Environmental Consulting: Rivervale, WA, Australia) p. 17
- Sprogis KR, Raudino HC, Rankin R, MacLeod CD, Bejder L (2016) Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Marine Mammal Science* **32**, 287–308. doi:10.1111/mms.12260
- Sprogis KR, Raudino HC, Hocking D, Bejder L (2017) Complex prey handling of octopus by bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science* **33**, 934–945. doi:10.1111/mms.12405
- Sprogis KR, Christiansen F, Raudino HC, Kobryn HT, Wells RS, Bejder L (2018a) Sex-specific differences in the seasonal habitat use of a coastal dolphin population. *Biodiversity and Conservation* **27**, 3637–3656. doi:10.1007/s10531-018-1618-7
- Sprogis KR, King C, Bejder L, Loneragan NR (2018b) Frequency and temporal trends of shark predation attempts on bottlenose

- dolphins (*Tursiops aduncus*) in temperate Australian waters. *Journal of Experimental Marine Biology and Ecology* **508**, 35–43. doi:10.1016/j.jembe.2018.08.008
- Sprogis KR, Videsen S, Madsen PT (2020) Vessel noise levels drive behavioural responses of humpback whales with implications for whale-watching. *eLife* **9**, e56760. doi:10.7554/eLife.56760
- Stensland E, Berggren P, Johnstone R, Jiddawi N (1998) Marine mammals in Tanzanian waters: urgent need for status assessment. *Ambio* **27**, 771–774.
- Stensland E, Angerbjörn A, Berggren P (2003) Mixed species groups in mammals. *Mammal Review* **33**, 205–223. doi:10.1046/j.1365-2907.2003.00022.x
- Sutton AL, Shaw JL (2021) Cumulative pressures on the distinctive values of Exmouth Gulf. First draft report to the Department of Water and Environmental Regulation by the Western Australian Marine Science Institution, Perth, Western Australia. p. 272. (Western Australian Marine Science Institution)
- Syme J, Kiszka JJ, Parra GJ (2021) Dynamics of cetacean mixed-species groups: a review and conceptual framework for assessing their functional significance. *Frontiers in Marine Science* **8**, 678173. doi:10.3389/fmars.2021.678173
- Symons J, Sprogis KR, Bejder L (2018) Implications of survey effort on estimating demographic parameters of a long-lived marine top predator. *Ecology and Evolution* **8**, 10470–10481. doi:10.1002/ece3.4512
- Taylor JG, Pearce AF (1999) Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. *Journal of the Royal Society of Western Australia* **82**, 57–65.
- Twiggs EJ, Collins LB (2010) Development and demise of a fringing coral reef during Holocene environmental change, eastern Ningaloo Reef, Western Australia. *Marine Geology* **275**, 20–36. doi:10.1016/j.margeo.2010.04.004
- UNESCO (2011) 'World heritage list – ningaloo coast.' (United Nations Education, Scientific and Cultural Organization) Available at <http://whc.unesco.org/en/list/1369/> [Accessed 2 December 2021]
- Urian K, Gorgone A, Read A, Balmer B, Wells RS, Berggren P, Durban J, Eguchi T, Rayment W, Hammond PS (2015) Recommendations for photo-identification methods used in capture–recapture models with cetaceans. *Marine Mammal Science* **31**, 298–321. doi:10.1111/mms.12141
- van Aswegen M, Christiansen F, Symons J, Mann J, Nicholson K, Sprogis KR, Bejder L (2019) Morphological differences between coastal bottlenose dolphin (*Tursiops aduncus*) populations identified using non-invasive stereo-laser photogrammetry. *Scientific Reports* **9**, 12235. doi:10.1038/s41598-019-48419-3
- Vanderklift MA, Pillans RD, Hutton M, De Wever L, Kendrick GA, Zavala-Perez A, Vergés A, Garthwin R, Oades D, McCarthy P, George K, Sampi T, George D, Sampi C, Edgar Z, Dougal K, Howard A (2021) High rates of herbivory in remote northwest Australian seagrass meadows by rabbitfish and green turtles. *Marine Ecology Progress Series* **665**, 63–73. doi:10.3354/meps13657
- Wang JY (2018) Bottlenose dolphin, *Tursiops aduncus*, Indo-Pacific bottlenose dolphin. In 'Encyclopedia of marine mammals'. 3rd edn. (Eds B Würsig, J Thewissen, KM Kovacs) pp. 125–130. (Academic Press: London, UK)
- Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In 'Current mammalogy'. (Ed. HH Genoways) pp. 247–305. (Plenum Press: New York, NY, USA and London, UK)
- Western Australia Biodiversity Conservation Act (2016) *Western Australia Biodiversity Conservation Act*, Version 00-f0-00. 206 pp. (Government of Western Australia, Department of Biodiversity, Conservation and Attractions) Available at www.legislation.wa.gov.au [Accessed 23 October 2021]
- WHCC (2005) Report on a proposal to nominate the north west cape – Ningaloo Reef area for inscription on the world heritage list. World Heritage Consultative Committee; Government of Western Australia, Perth, WA, Australia.
- Würsig B, Würsig M (1977) The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* **198**, 755–756. doi:10.1126/science.198.4318.755

Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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