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Moreton Bay; A previously unrecognized resting stopover for east-coast of Australia migrating humpback whales

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Humpback whales enter Moreton Bay, in southeast Queensland, Australia, each year during their annual migration. Little is known about the ecological significance of the bay for the humpback whale population. In a region characterised by rapid coastal and maritime development, as well as a growing humpback whale population, there is an urgent need to fill knowledge gaps surrounding the populations' seasonal distribution and habitat use in these coastal waters. This study procured the first detailed information regarding humpback whale distribution, behaviour, and habitat use within Moreton Bay, relative to the main east coast migratory corridor. It was found that on average 42.41% of the individuals observed on the southern leg of the migration entered the bay. 76.78% of pods entering the bay had accompanying calves and 47.82% of these pods were found to be resting or logging, a behaviour often associated with nursing, at the time of observation. These findings provide strong evidence for a previously undocumented role of Moreton Bay as a resting stopover for migrating humpback whales.

KEYWORDS

migratory species, resting stopovers, Southern hemisphere humpback whales, habitat use, energy balance, Moreton Bay, Antarctic climate change, sustainable development

1 Introduction

Southern hemisphere humpback whales (SHHW) (*Megaptera novaeangliae*) have evolved an extreme migratory life history that exploits the seasonal productivity of their principal prey item, Antarctic krill *(Euphausia superba)*. Their annual migrations between the Southern Ocean and equatorial breeding grounds are among the longest migratory journeys of any mammal on Earth, covering c.a.10 000 km (Andriolo et al., 2006; Zerbini et al., 2006). The migration is associated with five to nine months of fasting, representing a period of prolonged negative energy balance, exacerbated among females that simultaneously bear the energetic demands of pregnancy, parturition, and lactation.

Consequently, individuals may lose between one-third to one-half of their summer body mass during this time (Slijper, 1962; Dawbin, 1966; Lockyer and Brown, 1981; Baraff et al., 1991; Clapham et al., 1999). Understanding the species' energy conserving behaviours and strategies is of increasing importance in a rapidly changing Antarctic sea-ice ecosystem.

Managing energy balance is of particular importance for capital breeders such as SHHWs that fund the energetic cost of reproduction *via* temporally constrained periods of hyperphagia (Frisch, 1984; Gittleman and Thompson, 1988; Jönsson, 1997; Stephens et al., 2009). A single sub-optimal feeding season can carry individual fitness consequences, such as exhaustion, immunosuppression, and excessive mobilisation of lipophilic environmental toxins (Jönsson, 1997; Bengtson Nash et al., 2013; Bengtson Nash, 2018; Bengtson Nash et al., 2018). For sexually mature females, single or repeated sub-optimal feeding seasons may further carry population consequences *via* larger inter-pregnancy intervals, sub-optimal maternal provisioning of foetus' and dependent calves, or aborted pregnancies (Lockyer, 1986; Lockyer, 2007; Williams et al., 2013; Christiansen et al., 2014; Christiansen et al., 2016; Christiansen et al., 2018; Castrillon and Bengtson Nash, 2020; Christiansen et al., 2022).

Most SHHW populations are recovering from their post-whaling bottleneck, with some approaching pre-whaling numbers (Paterson et al., 2001; Noad et al., 2011). Concerns are, however, growing for many migratory species utilising increasingly impacted and fragmented habitats. Degradation of habitats through industrial, agricultural, and residential development, climate change, and pollution are some of the major threats that migratory species face (Robinson et al., 2005). Due to the extensive geographical range that these species occupy throughout their annual cycle (Runge et al., 2014; Schuster et al., 2019), conservation efforts are complicated by their migration across the jurisdictional limits of various nations (Ruckelshaus et al., 2008; Miller et al., 2018). The Convention on Conservation of Migratory Species of Wild Animals (CMS), also known as the Bonn Convention, was established in 1979 and seeks to conserve migratory species across their entire range. Conservation efforts primarily focus on breeding and feeding areas (Mehlman et al., 2005; Sheehy et al., 2011), with migratory corridors often neglected. Notably, many species of migratory ungulates, birds, and sea turtles (Shillinger et al., 2008; Harris et al., 2009; Murray et al., 2014; Runge et al., 2015), have dramatically declined in numbers despite well-established protected areas at both migration terminus points. For SHHWs that seasonally migrate between Antarctic feeding grounds, far removed from permanent human settlements, to urbanised coastal areas, the importance of safeguarding the entire migratory corridor of the species' range is particularly well exemplified.

The major drivers behind the seasonal migration of SHHWs out of Antarctica remain under active theoretical debate. Aside from diminished winter food availability, avoidance of predation at high latitudes (Corkeron and Connor, 1999), calf winning mass (Norris, 1967), and more recently skin molting (Pitman et al., 2020), are all theories that have been proposed. Such uncertainty regarding the fundamental ecology of the species, translates to carry-over uncertainty when forecasting the response of populations to rapidly changing functional habitats. In extra-Antarctic waters SHHWs are known to travel in close proximity to the coastline, preferring routes less than 200 m in depth, and generally within 20 km of the coast (Peel et al., 2018). Travel from northern breeding grounds, with accompanying newborn calves, is characterised by slower travel close to shore, with frequent resting stops (Simmons and Marsh, 1986; Mattila et al., 1989; Ersts and Rosenbaum, 2003; Félix and Guzmán, 2014). A 'stopover site' for migratory species is a site where the migration is paused to rest, conserve energy, and refuel (Mehlman et al., 2005; Dingle and Drake, 2007). Such sites, therefore, carry a disproportionate impact on an individual's mass gain and reproductive success, relative to time spent there (Drent et al., 2003; Smith and Moore, 2003; Schaub et al., 2008; Sheehy et al., 2011). The social and physiological drivers of humpback whale resting stopovers have previously been described (Chittleborough, 1953; Corkeron et al., 1994; Jenner et al., 2001; Braithwaite et al., 2012), and can summarised as a pause in migratory travel for mothers to engage in nursing and socialising with calves-of-the-year and older calves during the early stages of their southern migration (Franklin et al., 2011), contributing to the social development and high survival rates of calves and younger humpback whales (Franklin, 2014). Females with accompanying calves will favour lagoons with calm, shallow, and warm waters (Bruce et al., 2014; Ejrnæs and Sprogis, 2021) and utilise these areas as resting stopovers as the conditions facilitate coordination of nursing behaviour, and protect the calves from rough sea conditions, predators, and aggression from sexually active males (Craig et al., 2014; Bejder et al., 2019; Ejrnæs and Sprogis, 2021). Resting and nursing in these lagoon habitats, further plays a critical role in optimising energy balance of both mother and calf by minimising energy expenditure and maximising conversion of the mother's lipid rich milk to calf body mass. Recently, Videsen et al. (2017) quantified calf nursing dynamics and found that mothers and young calves were engaged in resting and nursing 20% of the total time observed. Resting stopover sites are therefore of key functional significance for SHHWs and even a relatively small amount of habitat disturbance or loss could carry negative population impacts (Runge et al., 2014) through for example disrupted nursing behaviour, or increased travel distance between suitable resting stopovers.

By comparison to feeding and breeding grounds, the ecological importance of resting stopovers have received less attention (Possingham et al., 2001; Wilson et al., 2006), yet the importance of properly identifying, characterising, and effectively managing human interactions in such areas are clear. For Australia's transient humpback whale populations, the Australian coastline offers numerous potential resting stopovers, yet only a few have been adequately characterised and formally recognized in the literature, notably Exmouth Gulf in Western Australia and Hervey Bay in Queensland (Jenner et al., 2001; Franklin et al., 2011; Franklin, 2014; Bejder et al., 2019).

Moreton Bay is located approximately 1700km south of the Great Barrier Reef, the breeding ground of the east coast of Australia migrating humpback whale population (Paterson and Paterson, 1984). It is a semi-enclosed embayment, sheltered by the large sand Islands, Moreton Island (Mulgumpin) and North

Stradbroke Island (Minjerribah) to the east. The average winter sea surface temperature in the bay is 20°C with an average depth of 8m (Pantus and Dennison, 2005). The natural physical environment of Moreton Bay offers similar conditions to other well-established SHHW resting stopovers. The bay, however, it is also located adjacent to one of Australia's fastest developing regions, and is the location of Australia's fastest growing container port, the Port of Brisbane. Humpback whales are regularly sighted within Moreton Bay, however, little is known about the proportion of the population that utilises the bay, their distribution, or their habitat use; all necessary parameters for effective management of human-wildlife interactions. This study sought to quantify these through systematic species abundance and distribution surveys across five consecutive years (2017 – 2021). In addition, surveys covered the main migratory corridor as a reference for findings. Here we describe the migratory dynamics and behaviours observed which are of broad relevance for the management of Moreton Bay, and similar embayment along Australia's migration corridors.

2 Materials and methods

2.1 Survey areas

Two spatial areas to the east and west of North Stradbroke and Moreton Islands, respectively (Figure 1) were surveyed over 5 consecutive years (2017 -2021). The two survey areas corresponded to 1) the sheltered Moreton Bay waters, between the Australian mainland and North Stradbroke and Moreton Islands (Area 1), and 2) the main Coral Sea migratory corridor, along the east coast of North Stradbroke and Moreton Islands (Area 2). Moreton Bay (Area 1) covered an area of 2284.9 km², from Mooloolaba in the north, to Thornlands in the south (approximately 95 km). This area has a high level of commercial and recreational maritime traffic and encompasses the main shipping channel across the bay, that facilitates high levels of commercial traffic to and from the Port of Brisbane, as well as several commercial ferry operating routes. The main migratory corridor (Area 2) study area was reduced between 2017 and 2018 to dedicate greater focus to Area 1, the area of study interest. In 2017, A1 covered 834.7 km^2 from the north of Moreton Island, south to the former Yarraman mine site on North Stradbroke Island (approximately 60 km). In 2018-2021 the northern boundary was moved south to the middle of Moreton Island (approximately 30 km), reducing the total survey area to 438 km² (Figure 1).

In order to explore localised habitat use, Area 1 was divided into three sub-areas (Figure 1). Sub-area *a*, with an area of 853 km², represents the northern part of Area 1, stretching from Mooloolaba to Moreton Island. Although part of this area belongs to Moreton Bay Marine Park, it extends beyond the enclosed bay area into open water with an ocean depth of more than 30 m. The area also encompasses the northern part of the shipping channel which traverses the bay from Mooloolaba to the Brisbane River mouth (90 km) and is dredged to maintain a minimum depth of 14 m. Sub-area *b* with an area of 1,076 km², covers the northern part of the Moreton Bay embayment stretching from the top of Moreton Island to the Port of Brisbane. This area is characterized by shallow waters with a depth from 1 to 15 m and encompasses the southern part of the shipping channel. Sub-area *c* with an area of 357 km², represents the southern part of Moreton Bay, with very shallow waters ranging from 1 to 10 m. This area does not include any part of the shipping channel, although coincides with the ferry routes of several vehicle and passenger ferries and is also the area with greatest recreational boating activity.

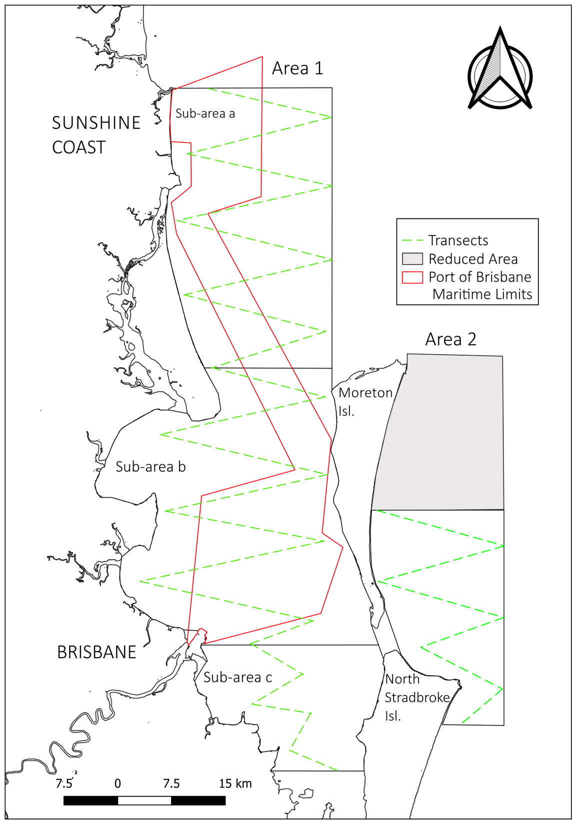

FIGURE 1
Survey Areas 1 (sub-areas *a*, *b* and *c*) and 2, depicted with the Port of Brisbane limits and transect design. The grey area depicts the survey area removed from 2017 to subsequent years.

2.2 Sampling design

Data collection was performed *via* boat-based line transect sampling methodology (Buckland et al., 1993). The transect design was mapped with an effective sampling band of 2.5 km in a zigzag formation (Figure 1). This systematic method incorporates observer effort thus allowing species presence and absence to be quantified. Transect sampling was performed at a travel speed of 8 knots, conducted against the direction of whales' migration to minimise the possibility of animals being recorded twice. Within Area 1, where the whales' direction of travel is less consistent, fluke and dorsal photos were obtained to exclude duplicate sighting recordings. Two observers positioned at the bow of the vessel at 2m above sea level, actively scanned with their naked eyes an angle of 100° each covering the starboard or port side from 90° to 10°

beyond the bow, thus ensuring animals on the transect line were detected, and satisfying distance sampling assumptions that the detection probability g(0) was 1. Upon sighting an animal, observers used an angle board to measure the radial angle, and estimated the radial distance to the sighting. These were recorded, as well as the boat's location using a Global Position System (GPS) and the sighting time. Depending on the pod distance, the decision to leave the transect and approach the pod to obtain detailed information on pod composition, size, behaviour, exact GPS position and photo-identification, was made. In these instances, when all the necessary information had been collected, the survey vessel returned to the point where the transect had been abandoned and the transect survey resumed. Depending on the number of trained personnel on the vessel the observers and the captain rotated each transect to rest. Surveys were only conducted under optimal sea conditions (Beaufort scale <4). Surveys were conducted for 5-6 weeks across the peak of each migration events at this latitude, i.e. during June – July (northward migration) and September – October (southward migration), when the whales are travelling to and from their winter breeding grounds respectively. Ancillary environmental data, such as sea state (Beaufort), wind direction and cloudiness were also collected at the start of each transect, as well as if conditions changed throughout. Whale sightings made whilst travelling along a transect were categorized as 'on effort' observations. When sightings were made whilst not travelling along a transect (e.g. from the launching point to the start of a transect point), these were categorized as 'off-effort' sightings.

2.2.1 Area correction

To account for both the change in the size of the reference area (Area 2) from 2017 to subsequent years, as well as the much larger survey area of Area 1 compared to Area 2, all gross sighting numbers were standardised by survey area covered. i.e.

$$Area\ \ Corrected\ \ N_{(A2)} = N_{(A2\ \ gross\ \ sighting\ \ number)} \times \frac{A1\ \ Area\ \ (km^2)}{A2\ \ Area\ \ (km^2)}$$

Unless stated otherwise in the text, all calculations have been based on area corrected values.

Whale density is defined as the number of individuals/km^2

2.2.2 Pod size and composition

Pod composition was categorised as outlined in Table 1 below.

2.2.3 Behaviour

For the purpose of this study, the different behaviours were categorised as outlined in Table 2.

To better understand the use of the Sub-areas of Area 1, a geographic information system (GIS) model of the study area was constructed using QGIS 3.22 (Quantum Geographical Information System) (QGIS, 2009) Australian coastal data were incorporated as a vector layer, and depth data were incorporated as a 5 m bathymetric grid. GPS coordinates of pods with accompanying calves resting and logging within the bay, were plotted to obtain these groups depth information.

2.3 Statistical analysis

A Chi-squared test of independence (*p=0.05*) was used to evaluate the significance of key pod composition and behavioural differences observed between study Areas 1 and 2.

3 Results

3.1 Survey effort

During the five-year sampling period, 41 survey days were conducted during the northern migration, between the 14th of June and 12th of July. Survey effort corresponded to 23 days in Area 1 and 18 days in Area 2. A total of 81 transects in Area 1 (1420.25 km) and 29 transects in Area 2 (425.21 km) were completed. A total of 49 survey days were conducted during the southward migration, between the 12th of September and 19th of October. Here, 31 days were dedicated to Area 1 and 18 days to survey Area 2. A total of 100.5 transects in Area 1 were completed (1851.1km) and 35 transects in Area 2 (534.94 km), (Table 3). No surveys were carried out during the northward migration of 2021.

TABLE 1 Pod descriptions used to characterise sighted pod compositions.

Pod type	Description
Solo (**S**)	A single individual
Pair (**P**)	Two adults (Pack et al., 2012)
Non-competitive pod (**NCP**)	More than two individuals, generally engaging in the same activity, but not displaying signs of competition
Competitive pod (**CP**)	A group of three or more individuals with or without a calf, in which the males physically compete with each other for proximity to the female, presumably for purposes of mating. (Tyack and Whitehead, 1983; Baker and Herman, 1984; Clapham, 1992)
Mother and calf (**MC**)	An adult-sized individual accompanied closely by a whale approximately 1/3 its length, often in contact with the adult-sized whale sometimes providing nurturant behaviours (Herman and Antinoja, 1977; Mobley and Herman, 1985)
Mother, calf and escort (**MCE**)	A mother-calf pair, accompanied by a non-calf, non-yearling adult male individual (Herman and Antinoja, 1977; Mobley and Herman, 1985).

*A distinction was also made between competitive and non-competitive pods with calves.

TABLE 2 Behaviour descriptions used to characterise sighting events.

Behaviour	Description
Travelling	Individuals moving in one direction at a relatively constant speed (Corkeron, 1995; Morete et al., 2003)
Breaching	A whale jumping out of the water, with more than 40% of its body leaving the water (Whitehead, 1985; Würsig and Whitehead, 2009)
Fin slapping	The whale raises one, or both of its pectoral fins clear of the water and slaps them repeatedly on the water surface (Whitehead, 1985; Würsig and Whitehead, 2009)
Tail slapping	Is a very energetic, and typically aggressive, action where the whale pivots on its head to lift its tail and peduncle clear of the water, only to crash the tail into the water with great force (Whitehead, 1985; Würsig and Whitehead, 2009)
Resting	When the whale is moving very slowly in no defined direction (Corkeron, 1995; Morete et al., 2003)
Logging	When the whale is completely at rest at the surface, a behaviour that is often associated with nursing (Müller et al., 1998)

For the purpose of representation, tail and fin slapping have been given the combined code of **TFS** due to the uncertainty in distinguishing differences from a greater distance.

All Area 2 transects were covered across the five years surveyed. By contrast, consecutive stretches of poor weather, combined with a high level of whale encounters, prevented completion of the transect network in Area 1 during the northward migration 2019, with approximately 16.72% of the transect distance in Area 1 not completed (3 transects). Similarly, the transect network in Area 1 was not completed during the southward migration of 2017 and 2018, with approximately 20% (4.5 transects) and 6% (1 transect) of the transect distance not completed, respectively.

3.2 Whale numbers and density

A total of 813 individual humpback whales were sighted during transect surveys associated with both the northward and southward field campaigns during 2017-2021 (Table 4). A further 536 individuals were sighted off-effort, whilst travelling to or from transects. Off-effort individuals were included only for the evaluation of whale distribution and habitat use, but not for abundance and density calculations.

During the northward migration, a total of 18 individuals across 10 sightings were observed in Area 1. This number rose to 397 individuals across 200 sightings on the southward migration in gross number terms.

On an area-corrected basis, the proportion of individuals observed in each area, during the five-year survey period, were as follows: on the northward migration, Area 1 animals corresponding to 3.66% of individuals observed during this period. By contrast, on the southward migration, individuals observed in Area 1 rose to 42.41% of individuals recorded during the migration.

The density of whales, as calculated by area and sub-areas, is presented in Table 4. Area 2 presented the highest density of whales during all northward migration campaigns, which was > ten times higher than the density in Area 1 during the same period. The low density of whales found in Area 1 during the northward migration, was concentrated entirely in Sub-area *a* (Figure 2). During the southward migration, the density of whales in Area 1 increased substantially (from 0.021 Individuals/km² to 1.113) with a maximum density across the survey period found in Sub-area *a* in 2017 (0.234), exceeding the density of whales in Area 2 during this same year (0.140).

TABLE 3 Summary of survey effort, including survey days and transect distance covered in each respective area during the northward and southward migrations of the five years survey.

Year	Survey Days				Number of Transects (Km)							
	Northwards		Southwards		Northwards				Southwards			
	A1	A2	A1	A2	A1		A2		A1		A2	
					No. of Transects	Km	No. of Transects	Km	No. of Transects	Km	No. of Transects	Km
2017	6	6	7	4	21	355.57	11	162.65	17.5	301.13	11	167.42
2018	5	5	6	4	21	376.2	6	88.03	20	341	6	89.6
2019	7	3	7	4	18	312.36	6	87.38	21	380.62	6	87.76
2020	5	4	6	3	21	376.12	6	87.15	21	377.05	6	87.41
2021	–	–	5	3	**No fieldwork was done here**				21	377.39	6	87.38
Total	23	18	31	18	81	1420.25	29	425.21	100.5	1777.19	35	519.57

'-' denotes that a survey was not performed.

TABLE 4 Humpback whale numbers and density in allocated areas per year, using on and off effort data.

		Northward Migration				Southward Migration			
		A1a	A1b	A1c	A2	A1a	A1b	A1c	A2
2017	No. of sightings	4	0	0	64	51	9	0	47
	No. of individuals	10	0	0	146	103	19	0	117
	Individuals/km^2	0.012	0.000	0.000	0.175	0.234	0.018	0.000	0.140
	Covered Area	852.480	1076.300	356.800	834.710	439.500	1076.300	356.800	834.710
	Area Corrected	27.374	0.000	0.000	399.654	281.948	52.010	0.000	320.271
2018	No. of sightings	2	0	0	69	36	13	2	95
	No. of individuals	3	0	0	153	69	30	7	212
	Individuals/km^2	0.004	0.000	0.000	0.349	0.091	0.028	0.020	0.484
	Covered Area	852.480	1076.300	356.800	438.000	761.620	1076.300	356.800	438.000
	Area Corrected	15.650	0.000	0.000	798.150	359.950	156.500	36.517	1105.933
2019	No. of sightings	1	0	0	29	25	4	0	49
	No. of individuals	1	0	0	66	43	10	0	105
	Individuals/km^2	0.002	0.000	0.000	0.151	0.050	0.009	0.000	0.240
	Covered Area	517.800	1076.300	356.800	438.000	852.480	1076.300	356.800	438.000
	Area Corrected	5.217	0.000	0.000	344.300	224.317	52.167	0.000	547.750
2020	No. of sightings	3	0	0	31	34	0	0	16
	No. of individuals	4	0	0	53	66	0	0	32
	Individuals/km^2	0.005	0.000	0.000	0.121	0.077	0.000	0.000	0.073
	Covered Area	852.480	1076.300	356.800	438.000	852.480	1076.300	356.800	438.000
	Area Corrected	20.867	0.000	0.000	276.483	344.300	0.000	0.000	166.933
2021	No. of sightings	No campaign undertaken				26	0	0	24
	No. of individuals					50	0	0	50
	Individuals/km^2					0.059	0.000	0.000	0.114
	Covered Area					852.480	1076.000	357.000	438.000
	Area Corrected					260.833	0.000	0.000	260.833

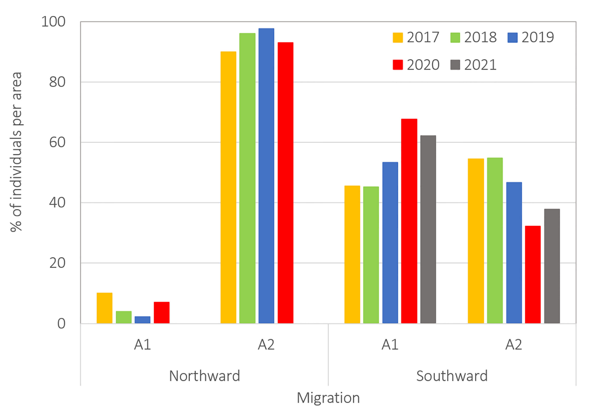

FIGURE 2
Area-corrected distribution of whales per survey area and migration.

3.3 Distribution

The spatial distribution of individuals changed markedly between the northward and southward migration timepoints. During the northward migration, distribution was highly biased toward Area 2. Only 3.66% (n=18, area corrected(ac)=69.10) of the observed northward migrating individuals were observed in Area 1, all of which were within Sub-area *a* (Figure 3). During the southward migration, the presence of individuals increased at least 10-fold in Area 1, corresponding to an average 42.41% (n=397, ac=1768.54) of the total individuals migrating south (35.28%, n=331, ac=1471.34 in Sub-area *a;* 6.25%, n=59, ac=260.67 in Sub-area *b*; and 0.87%, n=7, ac=36.51 in Sub-area *c)* (Figure 4). Although most of the sightings within Area 1 were concentrated in the northern part of the area, the whales also

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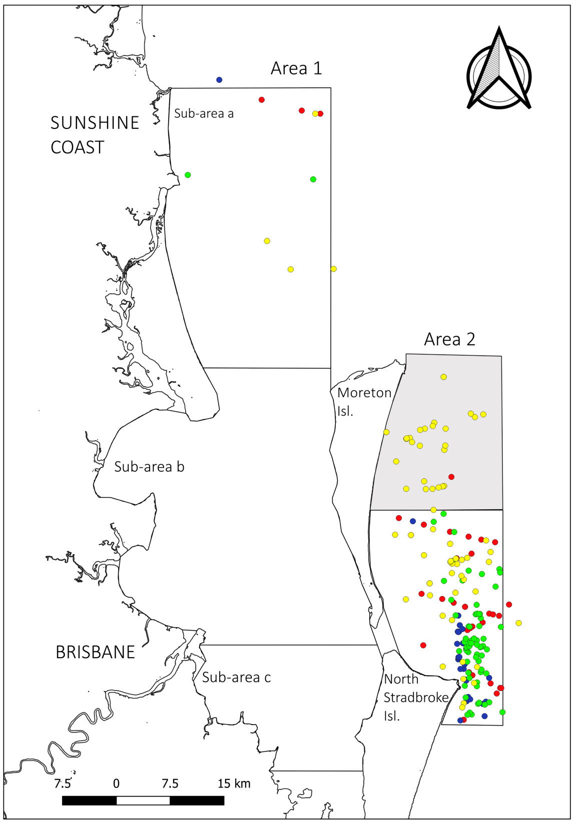

FIGURE 3
Compilation of humpback whale sightings during the northward migration over the five-year study period. In yellow 2017, in green 2018, in blue 2019, in red 2020 (no fieldwork occurred during 2021 northward migration). Shaded portion of A2 denotes the area covered in 2017 but not in subsequent years.

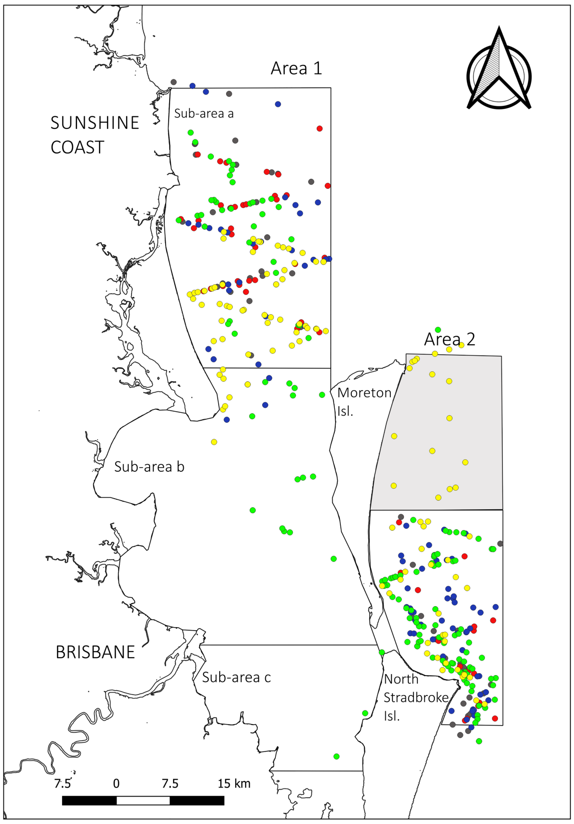

FIGURE 4
Compilation of humpback whale sightings during the southward migration across the five-year study period. In yellow 2017, in green 2018, in blue 2019, in red 2020 and in grey 2021. Shaded portion of A2 denotes the area covered in 2017 but not in subsequent years.

aggregate throughout the bay from the middle of Bribie Island, south to Moreton and North Stradbroke Islands. Sightings were made as far south as Cleveland, at the bottom of Area 1, decreasing in frequency from north to south. In the southern section of Moreton Bay, sightings were biased toward the east, in line with the sheltered coasts of Moreton Island. No sightings were made along the greater Brisbane coastline.

3.4 Pod size and composition

3.4.1 Pod size

The modal pod size in Area 1 increased from 2 (range 1-3) to 3 (range from 1-6) between the northward and southward migrations. In Area 2, the modal pod size was 2 (range 1-10) during both (Figure 5).

3.4.2 Pod composition

The predominant pod composition types during the northward migration by area were solo whales and non-competitive pods for Area 1, and non-competitive pods followed by pairs for Area 2. This dynamic changed during the southward migration, particularly for Area 1 where pods with calves made up 76.78% of all sightings, comprised of 47.32% mother-calf pairs (MC) and 25.89% mother-calf pairs accompanied by an escort (MCE). By contrast, MC pairs represented just 12.6% of observations for Area 2 on the southward migration, a defining difference between the two areas (X^2 (1, N=130) = 13.569; p=0.001). Instead, the predominant pod composition in Area 2 during the southward migration was pairs, representing 25.8% of observed pods in the area (Figure 6).

3.4.3 Calf pods

Of the pods observed with accompanying calves on the southward migration, more than half (61.6%) in Area 1 were MC pairs alone (Table 1), whereas mother-calf pairs were accompanied by an escort (Table 1) in 33.7% of the sightings. In a small percentage (4%) of sightings in Area 1 during the southward migration, a mother-calf pair were accompanied by a non-competitive pod (NCP+C) (Table 1) (Figure 7). By comparison to Area 1, MC pods made up 43% of calf pods in Area 2 during the same period, 34% had an accompanying escort, whilst 22% were mother calves travelling as part of a non-competitive pod (NCP+C).

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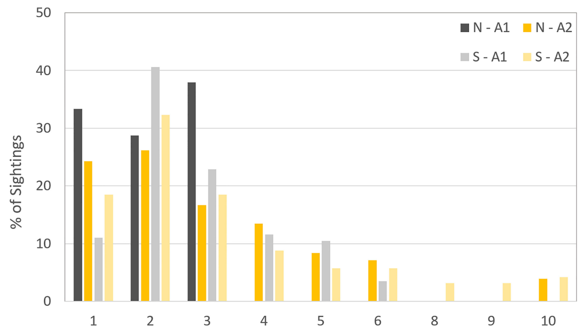

FIGURE 5
Pod size for both migrations in Area 1 and Area 2 during the five years survey.

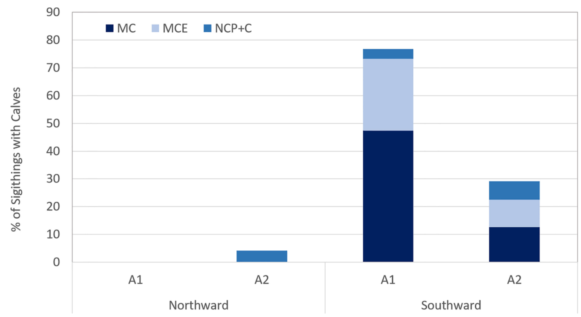

FIGURE 7
Percentage of sightings with calves.

3.5 Behaviour

Behavioural data was recorded on 276 pods in total, 99 during the northward migration and 177 during the southward migration. Travelling was the most common behaviour observed in Area 2 throughout the entire five-year study period (57.9% of individuals on the northward migration and 57.3% of individuals on the southward migration) (Table 2). By contrast, behaviours observed most frequently in Area 1 changed markedly between the two timepoints, coinciding with the influx of greater whale numbers into the area. During the northward migration, the dominant behaviours among the few whales entering Area 1 were breaching, tail and fin slapping and traveling. During the southward migration, the main behaviour observed was breaching (33.3%) followed by resting (28.8%) (Figure 8). Notably, resting whales made up only 4.45% of whales in A2 during the southward migration, compared to 28.88% of observed behaviours in A1, a highly significant ($p<0.00001$) difference between the two study areas.

3.5.1 Whale behaviours in area 1 sub-areas *a*, *b*, and *c* during the southward migration

In an attempt to better understand the nature and extent of habitat use by migrating humpback whales in Moreton Bay, whale behaviours were explored according to Sub-areas in Area 1 (Figure 9). Sub-areas *a* and *b* presented all coded behaviours. The predominant behaviour in Sub-area *a* was breaching (36.4%), followed by resting (24.2%), while resting (46.1%) was the most common behaviour in Sub-area *b*. Only two sightings were made in Sub-area *c* with traveling and resting as the recorded behaviours respectively.

3.5.2 Calf pods

When behaviours were further separated by pods with calves, it was found that 42.4% (n=39) of the pods with accompanying calves were observed resting and a further 5.4% (n=5) logging (Figure 10) at the time of observation. 76% (n = 38) of these sightings were made in water between 5 and 20 m (median 12.3m), and the remaining 24% (n=12) in a water depth greater than 20m (median 37.1m).

4 Discussion

Quantification of distribution, relative abundance, behaviour, and habitat of migrating humpback whales in Moreton Bay, over a five-year period, revealed substantive evidence that Moreton Bay is not only visited by a significant proportion of the annual migratory cohort, but that it also that it plays a functional role as a resting stopover for this population.

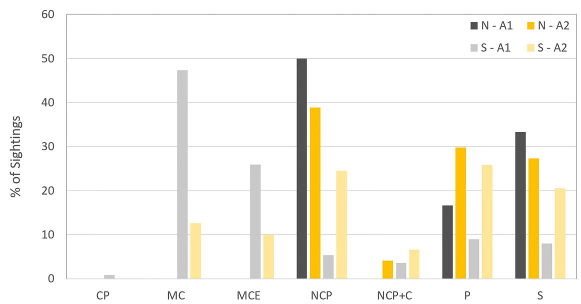

FIGURE 6
Pod composition for both migrations in Area 1 and Area 2 during the four years survey.

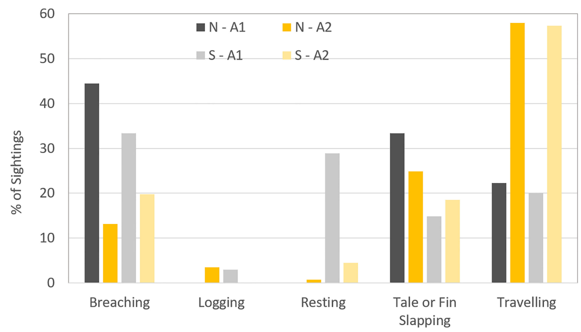

FIGURE 8
Pod behaviour for both migrations in Area 1 and Area 2 during the five years survey.

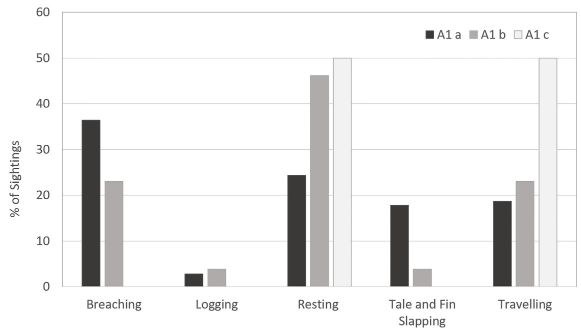

FIGURE 9
Whale behaviours according to sub-areas in Area 1 during the southward migration.

The unique significance of Moreton Bay, particularly to mothers and calves, was demonstrated by the marked change in spatial habitat use between the two migration time-points. Regardless of the survey year, there was a substantial increase in the number of whales entering the bay between the northward and southward migrations. The most notable feature of whale utilisation of Area 1 on the southward migration was the influx of pods with accompanying calves. Pods with calves made up 76.7% of sightings in Area 1 during the southward migration, whereas pods with calves amounted to less than half of the sightings in Area 2. By comparison to Area 1, consistent whale numbers were observed in Area 2 across both time periods, supporting the well-known role of Area 2 as a main migratory corridor of this population.

The role of Moreton Bay as a resting stopover for the east coast of Australia migrating humpback whale population was further supported by the observation that of the pods with accompanying calves observed within the bay, 47.82% were resting or logging at the time of observation. These findings suggest a unique functional role of Moreton Bay, particularly for mother-calf pairs. The shallow, and sheltered, lagoon-like habitat present in Moreton Bay match those described for resting stopovers in other regions in Australia, such as Hervey Bay (Franklin, 2014), Jervis Bay (Bruce et al., 2014), and Exmouth Gulf (Jenner et al., 2001; Bejder et al., 2019). These

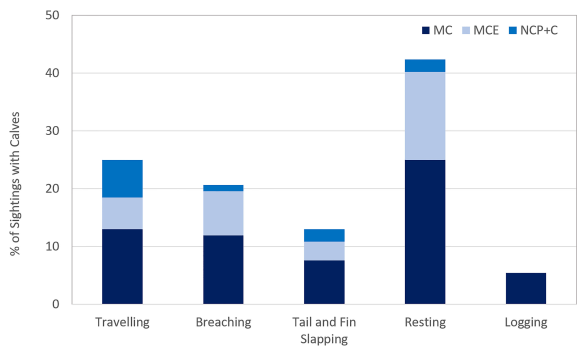

FIGURE 10
Behaviours recorded in Area 1, during the southward migration, in groups with calves. MC: mother and calf; MCE: mother, calf and escort; NCP+C: non-competitive pod and calf.

shallow lagoon-type habitats offer protection to calves from turbulent offshore conditions, predators, or aggression from sexually active males (Whitehead and Moore, 1982; Glockner and Venus, 1983; Smultea, 1994; Ersts and Rosenbaum, 2003; Craig et al., 2014). It has been suggested that premature conspecific social encounters increase the risk of elevated energy expenditure, interruption of nursing bouts, mistaken imprinting, or nursing attempts, potential separation of calves from mums, and calf injury or death (Jones and Swartz, 1984; Thomas and Taber, 1984; Smultea, 1994; Craig et al., 2014; Ransome et al., 2022). In addition, these waters facilitate effective coordination of nursing behaviour (Whitehead and Moore, 1982; Glockner and Venus, 1983; Smultea, 1994; Ersts and Rosenbaum, 2003). Stationary nursing, is energetically advantageous for both mother and calf; as it allows the mother to provide energy to her newborn while conserving as much of her own limited energy stores, and at the same time allows the calf to allocate energy for growth rather than movement (Harrison, 1969; Herman and Tavolga, 1980). While nursing behaviour is challenging to study in cetaceans since suckling occurs below the surface and milk transfer is difficult to verify, much of the literature describes that nursing behaviour occurs at a depth of 10 to 20 m (Glockner and Venus, 1983; Cartwright, 2005). In the current study, 76% of the pods with calves observed to be resting or logging were in waters between 5 and 20m in depth at the time of observation. Although this study did not attempt to detect or quantify nursing behaviour, the prevalent observations of resting and logging whales with calves in shallow waters, commensurate with nursing activity, provide strong indication that nursing occurs within the bay. The large proportion of time that mother-calf pairs dedicate to nursing and resting (Videsen et al., 2017; Bejder et al., 2019; Ejrnæs and Sprogis, 2021), is reflective of the critical importance of energy balance in this extreme migrating species, and the implications for individual fitness. For example, bigger calf size has been observed to be associated with better breath-holding ability, reduced vulnerability to predators, reduced heat loss during migration to high latitudes, and greater resilience to environmental variability (Christiansen et al., 2018).

Given the significant functional importance of resting stopovers for humpback whale energy balance, the discovery of Moreton Bay as a previously undocumented resting stopover is of significant conservation and management importance. Moreton Bay exhibits high levels of species diversity and richness but is also a region of high levels of all-year maritime traffic (Maritime Safety Queensland, 2005). As such, whales entering the bay must increasingly navigate anthropogenic stressors and threats such as disturbance and ship strike (Mayaud et al., 2022). Vessel proximity and underwater noise may disrupt critical nursing and resting behaviours (Pirotta et al., 2019), whilst whales engaged in resting and nursing are known to be less responsive to approaching vessels, and therefore more susceptible to ship strike (Laist et al., 2001). Ship strike risk is further exacerbated among calves and young that spend a greater amount of time at the surface (Laist et al., 2001; Lammers et al., 2013). Finally, vulnerability of this demographic group is further compounded by the low detectability of resting animals, and the restriction of avoidance by both whales and ships at shallow depths. Whilst further work is needed to understand the risk of humpback whale ship-strike from a range of vessel-categories in Moreton Bay

(Mayaud et al., 2022), the change in vessel traffic across Area 1 sub-areas *a, b* and *c*, likely provide clear clues as to the major risks associated with each sub-area. Sub-area *a*, which forms the entrance to the main Port of Brisbane shipping channel, is dominated by larger commercial vessels aggregating from deeper offshore waters to enter into the bay (Mayaud et al., 2022). The absence of the shipping channel in sub-area *c* results in a lack of large commercial vessels further south in the bay. By contrast, the protected inshore waters of sub-areas *b* and *c*, coincide with numerous islands, reefs, and fishing grounds making these areas particularly popular for smaller recreational vessels, as well as regular passenger ferry traffic.

5 Conclusions

Systematic abundance and distribution surveys of Moreton Bay, and the adjacent main migratory corridor, over the five-year period provided substantive evidence for the previously undocumented role of Moreton Bay as a resting stopover for the east coast of Australia migrating humpback whale population. Notably, the current study revealed a temporally constrained influx of whales into the bay during the southward migration, particularly by pods with accompanying calves. Pods with accompanying calves were further reported to be resting or logging 47.82% of the time, indicative of nursing behaviour. These findings present a local environmental management challenge for the sustainable use of this rapidly developing region. Further, they bring focus to the need for identifying similar resting stopover sites of these extreme migratory populations across their species range as continued degradation of key stopover sites will carry a disproportionate impact to species' energetic budgets.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Griffith University Animal Ethics Committee.

Author contributions

JC and SB conceived and designed the study. JC, GD, JA and RM Performed fieldwork and data collection. JC and SB analysed the data. JC took the lead in writing the manuscript with substantial support from SB. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that this study received funding from Port of Brisbane Pty Ltd. The funder contributed to late stage editing of the manuscript.

Publisher's note

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