Prevalence, Composition, and Behaviour of Humpback Whale (Megaptera novaeangliae) Groups Containing Multiple Mother-Calf Pairs in East Australia

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Abstract

Humpback whale (*Megaptera novaeangliae*) mothers and their calves predominantly avoid social interactions with conspecifics. However, observations from East Australia indicate that mother-calf pairs occasionally associate with other mother-calf pairs. We investigated the prevalence, composition, and behaviour of multiple-mother-calf (multi-MC) groups in East Australia from 2009 to 2023. In 2009 and 2010, data were collected from two tropical breeding areas (Port Douglas and the Whitsunday Islands) and two coastal migratory locations (Hervey Bay and Eden). No multi-MC groups were detected in Port Douglas out of 15 calf groups observed. Only one (4%) of 23 calf groups encountered in the Whitsunday Islands was a multi-MC group. In Hervey Bay, seven (4%) multi-MC groups were recorded out of 180 calf groups; while in Eden, seven (11%) out of 63 calf groups were multi-MC groups. Between 2009 and 2023, 978 calf groups were encountered in Hervey Bay over 12 years, including 56 (6%) multi-MC groups; while 39 (13%) out of 293 calf groups encountered in Eden over six years were multi-MC groups. Multi-MC groups exhibited more social behaviours compared to single MC groups. Social behaviour was common in both Hervey Bay and Eden; however, groups in Hervey Bay displayed lower arousal behaviours, consistent with the area's importance as a resting habitat for whales. We did not detect behavioural differences in multi-MC groups with or without escort whales. These findings suggest that humpback whale mothers may gradually

socialise their calves by forming multi-MC groups, with an increasing prevalence along the southerly migration route as calves mature. While multi-MC groups have only been detected in Australia to date, it is possible that they occur elsewhere, particularly if social development is a key driver of the phenomenon. Our results enhance our understanding of humpback whale mother–calf sociality and highlight the importance of migration routes for calf social development.

Key Words: behavioural observation, cetacean, migration route, resting area, social development, social dynamics

Introduction

Baleen whales generally do not form complex social networks (Tyack, 1986; Rendell et al., 2019). Apart from the association between a mother and its dependent calf, brief unstable social groups are common but rarely last more than a few hours (Tyack, 1986, 2022; Clapham, 1996; Rendell et al., 2019). Humpback whales (Megaptera novaeangliae), however, do exhibit some more social tendencies than other baleen species. "Groups" in humpback whales can be defined as a single whale or multiple individuals that are in close association (i.e., within two body lengths) and are demonstrating similar behaviours (Clapham, 2000). Stable social associations among adult humpback whales have been described on the feeding grounds, attributed to cooperative feeding strategies (Weinrich, 1991; Ramp et al., 2010), and Wray et al. (2021)

reported long-term pair associations of up to 12 y between humpback whales in British Columbia, Canada. Furthermore, humpback whales are well known for having highly complex communication signals (e.g., Payne & McVay, 1971; Noad et al., 2000; Dunlop et al., 2007; Cusano et al., 2021), a trait that is often associated with species that exhibit more intricate social associations (Jolly, 1966). While this information demonstrates that humpback whales exhibit some complex social behaviours, within a population, mother-calf pairs are typically less social than nonlactating adult females, adult males, and subadult animals (Mobley et al., 1988; Craig et al., 2014; Derville et al., 2018). The spatial and social segregation demonstrated by mother-calf pairs is common among cetaceans and may be motivated by a number of factors, including risk of injury to the calf, the potential for separation, energy conservation, or the interruption of crucial bond-forming processes (Smolker et al., 1992; Cartwright & Sullivan, 2009; Félix & Botero-Acosta, 2011).

Mother-calf pairs of humpback whales remain together for the duration of the lactation period, which lasts approximately 11 mo, at which time the calf is gradually weaned and separates from its mother (Clapham, 1996, 2000). Mothers and calves remain near one another with proximity decreasing as the calf matures (Szabo & Duffus, 2008). During the first year of a calf's life, it gains experience and learns behaviours from its mother, including familiarisation with migration routes and feeding areas (Weinrich, 1998; Szabo & Duffus, 2008; Rendell et al., 2019). In the breeding grounds, mothers with dependent calves typically have fewer social interactions than other adults (Mobley et al., 1988; Craig et al., 2014; Derville et al., 2018) and are generally found in shallower, coastal areas (Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Pack et al., 2017; Currie et al., 2018; Bejder et al., 2019). Craig et al. (2014) suggested that humpback whale mother-calf pairs in the Hawaiian breeding grounds sought out shallower areas to avoid unwanted male attention. Similarly, in a Southern Hemisphere feeding ground, mother-calf pairs were found to associate with fewer individuals or groups than nonlactating females and adult males (Barendse et al., 2013), while Ramp et al. (2010) found lactating females to associate with fewer groups than nonlactating females in a Northern Hemisphere feeding ground. Despite this wealth of information from breeding and feeding grounds, there remains a significant gap in our understanding of mothercalf sociality while migrating between the breeding and feeding grounds (Valsecchi et al., 2002).

The limited information we have on the social behaviour of migrating humpback whale

mother-calf pairs comes from Australia. Indeck et al. (2021) found that tagged mother-calf pairs migrating on the east coast of Australia typically segregated themselves from other whales, similar to observations made in breeding and feeding grounds elsewhere (e.g., Mobley et al., 1988; Barendse et al., 2013; Craig et al., 2014; Derville et al., 2018). However, in Hervey Bay, approximately 160 km north of where Indeck et al. (2021) made their observations, Franklin et al. (2021) reported mother-calf pairs associating with other mother-calf pairs. Similarly, a report from Exmouth Gulf, a known resting area for the Western Australian population of humpback whales (Chittleborough, 1953; Bejder et al., 2019), found that mother-calf pairs also associated together (Irvine & Salgado Kent, 2019). These observations suggest that mother-calf pairs in parts of Australia exhibit more social tendencies than has been previously reported.

Each year, the East Australian population of humpback whales migrate between their tropical breeding grounds in the Coral Sea in Queensland and their Antarctic feeding grounds (Smith et al., 2012). During the southern migration, Hervey Bay in Queensland acts as an important mid-migratory stopover for migrating whales, particularly for mothers and calves (Corkeron et al., 1994; Corkeron, 1995; Franklin et al., 2017; Stack et al., 2019). Mature males are not common in Hervey Bay (Franklin et al., 2017) and, as such, the shallow sheltered bay offers mothers a safe place to conserve energy and nurse their calves. Approximately 1,500 km south of Hervey Bay is Eden in New South Wales. Humpback whales have been recorded opportunistically feeding in waters off the Eden coastline on their southern migration (Stamation et al., 2007; Pirotta et al., 2021), highlighting another important location on the East Australian migration route. Individual humpback whales have been photographically identified in both Hervey Bay and Eden within the same year (Franklin et al., 2017), providing evidence that humpback whales that enter Hervey Bay during their southern migration may continue along the coastline and use the waters off Eden as the first accessible coastal feeding ground.

We had the unique opportunity, through observational data collected from two locations in the Coral Sea breeding grounds (Port Douglas and the Whitsunday Islands) and the two migration locations (Hervey Bay and Eden), to examine the occurrence of multiple-mother-calf (hereafter, multi-MC) groups in East Australia. Determining the prevalence of this behaviour both in the breeding grounds and during the southern migration allowed us to assess potential spatial patterns. Furthermore, given that Hervey Bay and Eden are progressively further south from the Coral Sea breeding grounds, it is plausible to assume that the calves would be more mature in these areas, allowing us to examine potential changes in mother–calf behaviour related to calf maturity. Our goal was to investigate the prevalence, composition, and behaviour of multi-MC groups to better understand the social dynamics of humpback whales.

Methods

Vessel-based surveys for humpback whales were conducted in four locations in East Australia between 2009 and 2023 (Figure 1). Port Douglas and the Whitsunday Islands are located within the Great Barrier Reef Marine Park in the Coral Sea—the primary breeding grounds for the East Australian humpback whales (Smith et al., 2012). Hervey Bay in Queensland and Eden in New South Wales are coastal locations where humpback whales are consistently observed while migrating south (Stamation et al., 2007; Stack et al., 2019).

Study Sites

Port Douglas (16° 27' 29" S, 145° 30' 14" E) is located towards the north of the Great Barrier Reef in the Coral Sea in Queensland (Figure 1). Data were collected in July and August 2009 and August 2010 near Cape Tribulation in the north to Cairns in the south, covering an area of approximately 3,400 km², with most survey effort concentrated around the Low Isles area. Depths in the survey area ranged from 5 to 35 m, and the prevalent substrate was sandy or muddy-bottom sediment (Lee Long et al., 1993). Some areas of seagrass beds are spread throughout the area but are not a predominant feature (Lee Long et al., 1993).

The Whitsunday Islands (20° 7' 37" S, 149° 0' 18" E) are comprised of 74 volcanic islands approximately 3,000 km² in area (Van Woesik, 1992) at the southern end of the Great Barrier Reef in the Coral Sea in Queensland, approximately 500 km south of Port Douglas (Figure 1). The benthic habitat consists of coral reef formed on rocky substrate or unstable pebble-like substrate (Hopley et al., 2007). The depth of the study area ranged from 5 to 60 m. Data were collected in August 2009 and during August and September 2010, with the majority of research effort surveying the Whitsunday Passage and the waters to the east and northeast of Hayman, Hook, and Whitsunday Islands.

Hervey Bay, approximately 700 km south of the Whitsunday Islands in southeast Queensland (25° 0' 58" S, 153° 6' 43" E), is a wide, shallow bay approximately 4,000 km² (Figure 1). It is bounded by mainland Australia to the south and west, and K'gari, a 126-km-long sand island, to the east with a shallow tidal delta at the southern end (Lee Long et al., 1993; Boyd et al., 2004). Depths within the bay generally do not exceed 40 m, with the average depth of the study area at approximately 18 m (Martinez et al., 2015). The substrate is predominantly sand or muddy bottom with some large areas of sea grass intermittently throughout the bay (Lee Long et al., 1993; Boyd et al., 2004). Survey effort was concentrated along the eastern side of the bay in an area known as Platypus Bay between July and October from 2009 to 2017 and from 2021 to 2023.

Eden in southern New South Wales (37° 4' 44" S, 149° 56' 46" E) represents the southernmost study area, approximately 1,500 km south of Hervey Bay (Figure 1). The survey area consisted of an inshore region known as Twofold Bay, with depths averaging 20 m as well as an area approximately 5 to 15 km offshore from the mouth of Twofold Bay with depths ranging from 20 to 95 m (Oliver & Tamura, 2022). The substrate is typified by a broad range of sandy sediment types (Oliver & Tamura, 2022). Survey effort occurred during September and October 2009 and 2011 and in October 2010, 2013, 2014, and 2023.

Data Collection

Survey effort varied across study sites and between years. Surveys were conducted between July and November with variable start and end dates at each location based on arrival and departure times of humpback whales in each area and in each year. The majority of data were collected in Hervey Bay and Eden, with 2009 and 2010 representing the only years when data were recorded from all four locations in the same year. Humpback whales are generally not found in Hervey Bay on the northern migration (Corkeron et al., 1994); and to maintain consistency, any data recorded in Eden that were assumed to be from whales travelling north were excluded. To do this, GPS tracks of all encounters were plotted, and those with an overall northerly trajectory were excluded (n = 1). Data were recorded over a range of platforms using different survey designs; however, the general methods and data collected for each encounter remained consistent throughout the course of the study. Dedicated research surveys were conducted on a range of rigid inflatable vessels across the four locations. In 2009 and 2010, dedicated research surveys were conducted in all four locations. In Hervey Bay, dedicated research surveys were also conducted in 2011, 2012, 2014-2017, and 2021-2023. In Eden, dedicated research surveys were conducted in 2011, 2013, and 2023. In 2013, linetransect surveys were conducted in Hervey Bay following methods detailed in Martinez et al.

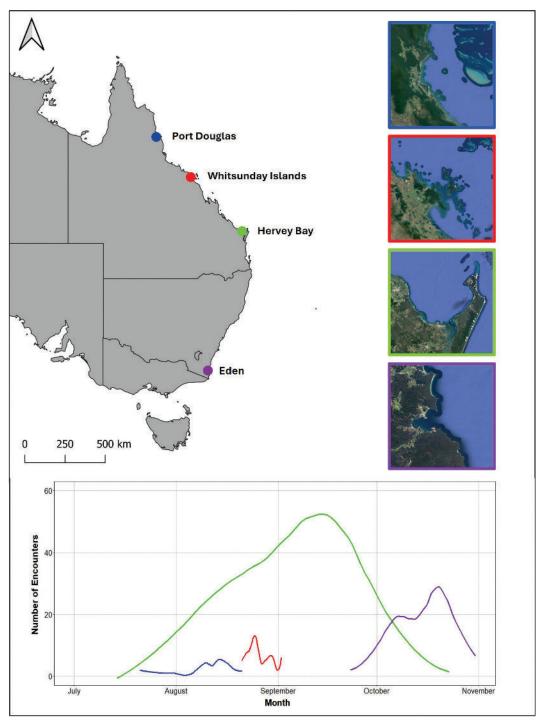


Figure 1. (Top) A map of the four study sites in East Australia: Port Douglas (blue), the Whitsunday Islands (red), Hervey Bay (green), and Eden (purple); and (bottom) temporal distribution of sighting locations, pooled across all available data and years. The graphs illustrate the peak survey effort periods for each site, showing distinct sighting trends over time. For ease of interpretation, smoothing was applied using the loess method with the 'geom_smooth()' function in *R*, Version 4.3.3. Location inset maps: *Google Earth Pro*, Version 7.3.6 (2024), East Australia (www.google.com/earth/index.html).

(2015). Data were also collected opportunistically from commercial whale-watch vessels used as platforms of opportunity. In Hervey Bay, data were recorded from whale-watch vessels in 2009-2012, 2014, 2021, and 2022. In Eden, data were recorded from whale-watch vessels in 2009-2011, 2013, and 2014. Across all survey methods, when a group of whales was encountered, information on location, group size, group composition, and behaviour was recorded on approach. Photographs of the tail flukes and dorsal fins of individuals were also taken for identification purposes as part of an ongoing, long-term population monitoring programme dating back to 1984 (e.g., Kaufman et al., 1987; Stack et al., 2019). During this time, a focal follow of the group was undertaken to determine the overall behaviour of a group during an encounter and to ensure group size and composition information was accurate. Encounter location (latitude and longitude) was recorded when the vessel was ≤ 100 m from the focal group.

Group Composition

Humpback whale "groups" were defined as either single whales or multiple whales swimming within two body lengths of each other, moving in the same direction and demonstrating similar behaviours (Clapham, 2000). Group size and composition were determined from vessel-based observations during focal follows. Age class of individuals was assigned by length estimates from visual observations. Adapted from Chittleborough (1959), individuals that were visually estimated to be 11 m or more in length were classified as adults, and those that were less than 11 m in length were classified as subadults. Any individuals that were less than 9 m in length and in close, consistent association with an adult were classified as calves. Any adults that were in close, consistent association with a calf were classified as mothers. When two or more mothers with their respective dependent calves were recorded swimming within two body lengths of each other, moving in the same direction, and demonstrating similar behaviours, they were called multi-MC groups (Figure 2). Single mother-calf groups and multi-MC groups could be associated with additional individuals (adults or subadults) termed "escorts." If a group was joined by additional individuals, an "affiliation" was recorded and classified as a new group. Similarly, if an individual left a group, a "disaffiliation" was recorded resulting in a new group. Only group composition at the time of the initial observation was included; all affiliations and disaffiliations were excluded from the analyses. To determine the prevalence of multi-MC groups in East Australia, the proportion of multi-MC groups in all calf encounters was calculated

for each location for 2009 and 2010 and for all years that surveys were undertaken in Hervey Bay and Eden.

Behaviour

The overall behaviour state of a group was recorded at the start of an encounter when the group was initially approached and again at the end of the encounter. Group behaviour states included feeding, resting, milling active, surface active, travelling, and other. These behaviour states could contain a range of behavioural events (see Table 1 for a detailed description). For the current study, only the behaviour recorded at the start of an encounter was used to ensure the vessel presence did not alter the behaviour of the group. We calculated the proportion of each behaviour across encounters for all locations and compared the behaviour of single calf groups to multi-MC groups, and multi-MC groups both with and without escort whales. We further compared multi-MC group behaviour in Hervey Bay and Eden. To test if behaviour differed significantly between groups, we used the Chisquared test (Pearson, 1900) if expected frequencies were all > 5, and Fisher's Exact Test (Fisher, 1934) if expected frequencies were < 5 (Fleiss, 1981).

Results

Survey Effort – All Locations: 2009-2010

During 2009 and 2010, 700 humpback whale encounters were documented over 132 surveys across the four sites. In Port Douglas, where 36 surveys were undertaken, 48 humpback whale groups were encountered. The fewest surveys (n= 11) were conducted in the Whitsunday Islands, with 44 encounters recorded. There were 376 encounters recorded in Hervey Bay over 45 surveys and 232 in Eden over 40 surveys (Table 2).

Survey Effort – Hervey Bay & Eden: 2009-2023

Between 2009 and 2023, survey effort in Hervey Bay occurred in 12 y across 651 surveys, resulting in 2,245 humpback whale group encounters. In Eden, 105 surveys occurred in 6 y, resulting in 541 humpback whale group encounters (Table 2).

Calf Group Composition – All Locations: 2009-2010

During 2009 and 2010, 40.1% (n = 281) of encounters contained at least one calf, and of those calf groups, 5.3% (n = 15) were multi-MC groups. In Port Douglas, the most northerly site, 31.3% (n = 15) of encounters included a calf, and all were single calf groups. In the Whitsunday Islands, 52.3% (n = 23) of encounters comprised



Figure 2. (A) Example of multiple-mother-calf pair behaviour showing three mother-calf pairs slowly travelling together in Hervey Bay, Queensland; and (B) two calves interacting while their mothers swim alongside in Eden, New South Wales. (Photos provided by the Pacific Whale Foundation Australia)

Behaviour state	Definition
Feeding	Group is observed consuming or actively chasing prey items (does not include nursing calves).
Resting	Extended time at the surface with no consistent direction of travel. The group remains in the same location displaying sedate behaviours.
Milling active	Extended time at surface with no consistent direction of travel. Involved in a variety of low arousal surface active behaviours.
Surface active	Displaying high arousal surface behaviours (e.g., head lunge, head slap, pectoral fin slap, tail slap, tail swish, peduncle throw, breach). The group can remain in the same location or be moving in a steady direction.
Travelling	Steady, directional movement where the group is moving in the same direction.
Other	Behaviour does not fall within the above categories.

Table 1. Definitions of behaviour states recorded when groups of humpback whales (*Megaptera novaeangliae*) were encountered (adapted from Di Clemente et al., 2018; Fiori et al., 2019)

Table 2. Details on humpback whale surveys in East Australia. The table is split into two sections: the first uses data from 2009 and 2010 when all four study locations were sampled, and the second focuses on all available data from Hervey Bay and Eden between 2009 and 2023. Details include the number of vessel surveys, the number of humpback whale encounters, calf presence within a group, and the number of calf groups that were single- and multiple-calf groups.

Location	Surveys	Encounters	No calf present (%)	Calf present (%)	Single calf (%)	Multi-MC (%)
			All locations (2	2009-2010)		
All	132	700	419 (59.9)	281 (40.1)	266 (94.7)	15 (5.3)
Port Douglas	36	48	33 (68.8)	15 (31.3)	15 (100.0)	0 (0.0)
Whitsunday Islands	11	44	21 (47.7)	23 (52.3)	22 (95.7)	1 (4.4)
Hervey Bay	45	376	196 (52.1)	180 (47.9)	173 (96.1)	7 (3.9)
Eden	40	232	169 (72.8)	63 (27.2)	56 (88.9)	7 (11.1)
			Hervey Bay & Ede	en (2009-2023)		
All	756	2,786	1,515 (54.4)	1,271 (45.6)	1,176 (92.5)	95 (7.5)
Hervey Bay	651	2,245	1,267 (56.4)	978 (43.6)	922 (94.3)	56 (5.7)
Eden	105	541	248 (45.8)	293 (54.2)	254 (86.7)	39 (13.3)

at least one calf, and one was a multi-MC group (4.4% of calf groups). In Hervey Bay, where the most humpback whale encounters were recorded during 2009 and 2010 (n = 376), at least one calf was recorded in 47.9% (n = 180) of encounters. Of the calf groups in Hervey Bay, seven (3.9%) were recorded as multi-MC groups. In Eden, the most southerly location, 27.2% (n = 63) of encounters had a calf present, of which 11.1% (n = 7) were recorded as multi-MC groups (Table 2).

Calf Group Composition – Hervey Bay & Eden: 2009-2023

In Hervey Bay and Eden, between 2009 and 2023, there were 2,786 humpback whale encounters, of which 45.6% (n = 1,271) had at least one calf present. Of the calf groups, 7.5% (n = 95) were multi-MC groups. In Hervey Bay, 43.6% (n = 978) of the 2,245 humpback whale encounters recorded included at least one calf. Of the calf groups, 5.7% (n = 56) were multi-MC groups. In Eden, 541

humpback whale encounters were reported. Of these, 54.2% (n = 293) were calf groups, of which 13.3% (n = 39) were multi-MC groups (Table 2).

Behaviour – Multi-MC Groups vs Single Calf Groups

When comparing the behaviour of multi-MC groups and single calf groups in all locations, we found significant differences ($\chi^2 = 43.34$, df = 5, $p \le 0.001$). Multi-MC groups exhibited more of the social behaviours than single calf groups with surface active behaviour accounting for 43.0% of observed behaviour in multi-MC groups and 26.3% in single calf groups, and milling active behaviour accounting for 14.0% of multi-MC group behaviour. Single calf groups were recorded travelling more (47.4% of the time) than multi-MC groups (35.5% of the time). Notably, multi-MC groups spent very little time resting (3.2%), while single calf groups were resting 18.4% of the time (Figure 3).

Behaviour - Hervey Bay vs Eden

There were significant differences in the behaviour of multi-MC groups in Hervey Bay and Eden ($\chi^2 = 11.23$, df = 5, p = 0.047). In Hervey Bay, travelling was the most commonly

observed behaviour in multi-MC groups (45.3%), with surface active (35.8%) and milling active (17.0%) behaviour following. In Eden, however, surface active behaviour was the most commonly observed behaviour in multi-MC groups (51.3%), with travelling accounting for less than a quarter (23.1%) of observed behaviour. Milling active behaviour (10.3%), feeding (7.7%), and resting (5.1) comprised most of the remaining behaviour observed in Eden. There was no feeding behaviour observed in Hervey Bay, and multi-MC groups spent 1.8% of their time resting (Figure 4).

Behaviour - Escort Present vs No Escort

There was no significant difference in the behaviour of multi-MC groups whether an escort was present or not across all locations (Fisher's Exact Test, p = 0.445; Figure 5). We recorded more surface active behaviour (46.3%) and less travel (32.8%) in multi-MC groups without escorts than with an escort (surface active: 34.6%; travelling: 42.3%). Resting was not recorded in the presence of escorts, whereas 4.5% of multi-MC groups without escorts rested. Feeding was more commonly recorded when escorts were present (7.7%) than when they were not (1.5%).

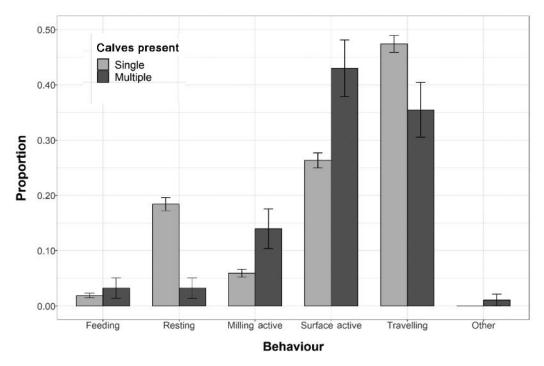


Figure 3. The behaviour of single calf groups (light grey) and multi-MC groups (dark grey) between 2009 and 2023 across all locations

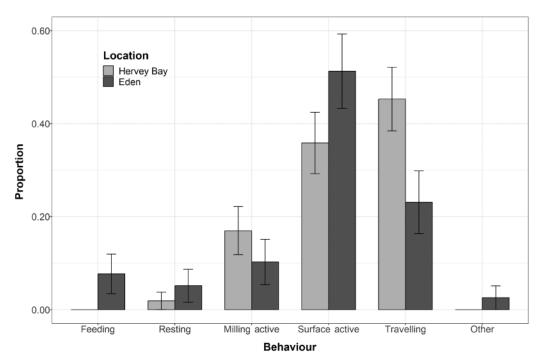
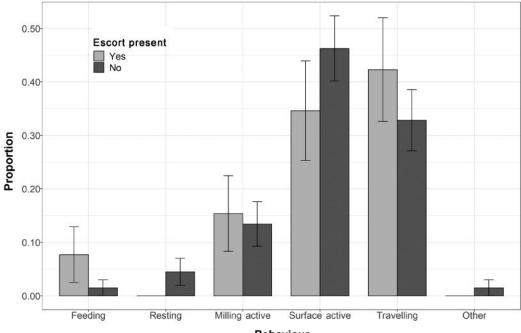


Figure 4. The behaviour of multi-MC groups in Hervey Bay (light grey) and Eden (dark grey) between 2009 and 2023



Behaviour

Figure 5. The behaviour of multi-MC groups with (light grey) and without (dark grey) escort whales present between 2009 and 2023 across all locations

Discussion

Humpback whale mother-calf pairs are typically regarded as the least social cohort in a population and have been reported to avoid interactions with other whales in the breeding and feeding grounds (Mobley et al., 1988; Ramp et al., 2010; Barendse et al., 2013; Craig et al., 2014; Derville et al., 2018). Herein, we present details of social interactions between multi-MC groups on the east coast of Australia. Similar to research from other humpback whale breeding areas (e.g., Mobley et al., 1988; Craig et al., 2014; Derville et al., 2018), we found a low proportion of social interactions between mother-calf pairs in two sites in the East Australian breeding grounds, only recording one multi-MC group in the Whitsunday Islands during 2009 and 2010. During the same period, 3.9% of calf groups in Hervey Bay and 11.1% in Eden contained two or more calves. These proportions increased when considering data from 2009 to 2023, with multi-MC groups accounting for 5.7% of calf groups in Hervey Bay and 13.3% in Eden.

Hervey Bay is a migratory stopover site commonly used for resting as the whales travel south (Corkeron et al., 1994; Corkeron, 1995; Franklin et al., 2011; Stack et al., 2019), while Eden is an area where whales have been recorded opportunistically feeding before heading to Antarctic waters (Stamation et al., 2007; Pirotta et al., 2021). Although limited records of calves born outside of the breeding areas exist (e.g., Torre-Williams et al., 2019), typical migratory patterns of the East Australian humpback whales indicate that the majority of calves are born in the Coral Sea breeding area (Smith et al., 2012). Therefore, the calves in Port Douglas and the Whitsunday Islands should generally represent the youngest calves, those in Hervey Bay would be of an intermediate age, and those in Eden would represent the oldest calves. While it is possible that the local geographic and bathymetric features in these areas may facilitate the forming of multi-MC groups, the higher prevalence of multi-MC groups with increasing latitude suggests that there may be a link to calf maturity.

The role of social interactions in the development of young animals is well-documented (see Galef & Laland, 2005, for a review of social learning in animals). There are selective pressures on juvenile animals to ensure they have the social skills needed to maximise their fitness when they reach maturity (Joffe, 1997). Important strategies such as predator avoidance, foraging success, mate choice, and movement patterns are all influenced by social interactions (Galef & Laland, 2005). As humpback whale mother–calf pairs do not typically associate with other whales in the breeding grounds when the calf is at its youngest (Mobley et al., 1988; Craig et al., 2014; Derville et al., 2018), the migration route may present valuable opportunities for the calf to develop social skills before the pair separates.

The behaviour of multi-MC groups across all locations was characterised by a high degree of surface active behaviour (43.0%) and milling active behaviour (14.0%) (Figure 3). Humpback whales are well-known for demonstrating surface active behaviour such as breaching, pectoral fin or tail slapping, and head lunging, and these have been recorded in a range of different social contexts. For example, pectoral fin and tail slapping can be used by females to convey their presence to males in the breeding grounds (Herman, 2017) and as a form of short-range, within-group social communication while migrating (Kavanagh et al., 2016). Surface active behaviours have also been associated with agonistic interactions (Lunardi et al., 2010). However, in Hervey Bay, the social behaviour of humpback whales is typically non-agonistic in nature (Franklin et al., 2021; McCulloch et al., 2021). The surface active behaviour recorded from multi-MC groups in the current study may, therefore, be a form of withingroup communication, similar to what Kavanagh et al. (2017) observed elsewhere on the east coast of Australia. Coupled with our findings that multi-MC groups are more common when calves are older and less vulnerable, it is possible that these groups are formed to facilitate calf social development.

The difference in the proportion of milling active and surface active behaviours observed between Hervey Bay and Eden (Figure 4) may reflect how each site is utilised during the whales' migration. Hervey Bay is utilised as a mid-migratory stopover where whales spend time resting (Corkeron et al., 1994; Corkeron, 1995; Franklin et al., 2011; Stack et al., 2019). As such, the higher proportion of milling active behaviour, a low arousal form of social behaviour, compared to Eden, may represent a behaviour state that combines both social and resting aspects. As calves are active at the surface, the mothers may take the opportunity to rest or vice versa. The higher proportion of surface active behaviour, a higher arousal social behaviour, in Eden could be attributed, in part, to a difference in the environmental parameters of the areas. The waters off Eden are more exposed to the Southern Ocean than Hervey Bay, and wind speeds are often much higher (Thom & Hall, 1991). Dunlop et al. (2010) found that humpback whales increased their use of surface active behaviours in higher wind speeds when background sound levels increased. While the data

for this study were collected in similar conditions across sites, the wind speeds are generally lower in Hervey Bay (Thom & Hall, 1991); however, without formal testing of this theory, we cannot say for certain. The presence of feeding behaviour observed in multi-MC groups in Eden is logical considering it is a known opportunistic feeding area (Stamation et al., 2007; Pirotta et al., 2021) and, in Hervey Bay, the whales are not thought to feed (Corkeron et al., 1994).

Another potential reason for the formation of multi-MC groups is it may afford increased safety from predators. Animals can form groups to protect themselves and their young from predators to benefit from the "dilution effect" (Foster & Treherne, 1981; Mooring & Hart, 1992) or the "confusion effect" (Hamilton, 1971), and/or to increase overall vigilance while decreasing individual vigilance (Caine & Marra, 1988). Killer whales (Orcinus orca) predate on humpback whale calves in Australia and have been suggested as a factor influencing the migration of whales worldwide (Corkeron & Connor, 1999). Naessig & Lanyon (2004) reported 17% of humpback whales in East Australia had killer whale scars on their bodies; and they detailed two individuals, one in the Coral Sea breeding grounds and one in Queensland south of Hervey Bay, that had fresh killer whale scars. Therefore, the formation of multi-MC groups may be linked to predator presence; however, more research in this area would be needed to determine if this is the case.

Mothers may also form groups with other mothers and calves to avoid interactions with escorts. Females with calves increase their energy expenditure in the presence of escorts (Cartwright & Sullivan, 2009), and the potential for mother-calf separation is also increased (Pack et al., 2002). Therefore, multi-MC groups may be formed as protection from escort attention, similar to how groups are formed as an antipredator response (e.g., Hamilton, 1971; Foster & Treherne, 1981; Caine & Marra, 1988; Mooring & Hart, 1992). However, our results found that the prevalence of multi-MC groups was lowest in the Coral Sea breeding area, where only one multi-MC group was recorded. The breeding area is where females are most likely to be approached by males for the purpose of mating. In Hervey Bay, however, where more multi-MC groups were recorded, there are relatively few adult males to serve as escorts (Franklin et al., 2011), and aggressive behaviour is uncommon (Franklin et al., 2021; McCulloch et al., 2021). There were some differences in the behaviour of whales in the presence of escorts, such as less resting and milling active behaviour and more surface active behaviour, but the overall proportion of observed behaviours was

not significantly different (Figure 5). Given these results, it is unlikely that the population of humpback whales along the east coast of Australia form multi-MC groups as a strategy to protect calves from interactions with escort whales, adding further support to the theory that they are formed as a way to develop calf social skills.

Given how important social development is to young animals (Galef & Laland, 2005), it is surprising that multi-MC groups appear to be unique to Australia. To our knowledge, there are no published reports of multi-MC groups from any other humpback whale population outside of Australia. East Australia offers an ideal opportunity for studying migrating humpback whales as approximately 2,500 km of coastline runs parallel to a large portion of the migratory corridor (Andrews-Goff et al., 2023). As a result, the opportunity to observe different behaviours and group compositions during different stages of migration differs from populations elsewhere that often cross ocean basins that are largely inaccessible to direct observations (e.g., West Indian Ocean: Fossette et al., 2014; North Atlantic: Kennedy et al., 2014). Furthermore, the population has made a significant recovery from the impacts of commercial whaling with the most recent population estimate standing at approximately 25,000 individuals (Noad et al., 2016). This large population, coupled with the close proximity of the migration route to the coast, provides ample opportunity for researchers to access and study this population; and it may be that this behaviour occurs elsewhere but is yet to be documented.

The presence of multi-MC groups during the humpback whale southerly migration along the coast of East Australia raises some conservation concerns. In Australia, there has been a steady increase in the use of waterways over the last few decades (O'Neill & Leigh, 2007; Burgin & Hardiman, 2011). Vessel strikes are regarded as one of the primary threats to whales worldwide (Laist et al., 2001; Peel et al., 2018; Rockwood et al., 2018), and information from Queensland, East Australia, suggests that vessel strikes on humpback whales may be increasing in frequency (Meynecke & Meager, 2016). Given that multi-MC groups demonstrate high levels of surface behaviour, the potential for vessel strikes may be increased, particularly in Hervey Bay, where less conspicuous surface behaviours were recorded than in Eden. As such, conservation and education efforts should incorporate multi-MC groups to ensure that ocean goers are aware that these groups are known to occur in certain areas along the migration pathway.

Our findings highlight the importance of continued research on humpback whales, particularly in less studied areas such as migratory pathways. Future studies of multi-MC groups should expand spatial and temporal coverage to better understand the mechanisms behind the formation and persistence of multi-MC groups. Uncovering new information regarding humpback whale populations, such as the prevalence, composition, and behaviour of multi-MC groups in East Australia, allows us to continue to build our knowledge base on populations which can ultimately lead to better-informed conservation measures to ensure populations are maintained at favourable conservation status.

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