Aquatic Mammals 2022, *48*(3), 273-286, DOI 10.1578/AM.48.3.2022.273

Calf-Directed Aggression as a Possible Infanticide Attempt in Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

Leanne R. Rosser,[1] Tadamichi Morisaka,[2] Yoko Mitani,[3] and Takeshi Igarashi[1]

[1]*Mutsu Bay Dolphin Research, Mutsu, Aomori, Japan*
E-mail: leannerachaelrosser@gmail.com
[2]*Cetacean Research Centre, Graduate School of Bioresources, Mie University,*
1577 Kurimamachiya-cho, Tsu, Mie 514-8507, Japan
[3]*Field Science Centre for Northern Biosphere, Hokkaido University,*
20-5 Benten-cho, Hakodate, Hokkaido 040-0051, Japan
Current address for Yoko Mitani: Wildlife Research Centre, Kyoto University,
2-24 Tanaka-Sekiden-cho, Sakyo, Kyoto 606-8203, Japan

Abstract

We report the first case of conspecific calf-directed aggression in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as a possible infanticide attempt in Mutsu Bay, Japan. Our observation of a 75-minute-long persistent attack on a neonate was performed by 10 attackers (4 adult males, 1 possible male, and 5 of unknown sex) and left the neonate with visible injuries. Only one individual was recorded for the entirety of the event and was regarded as the possible mother, displaying protective behaviours towards the neonate as well as being the target of coercive guarding and sexual behaviours, such as mounting, by the attackers. The observation featured a distinct group composition change in which, after 50 minutes, the attack was taken over by a new group of attackers. There was a brief overlap between the groups in which some dolphins from the first group surfaced with the second. Excluding the mother and calf, only two individuals that were observed towards the end of the first group attack remained with the second group until the end of the observation. The first group of attackers did not make further aggressive attempts on the neonate or presumed mother, and no conflict between the two groups was witnessed. The second group continued the attack with significantly increased aggression and a greater array of behavioural types than the first, often dividing into two approximately 5- to 10-m distanced subgroups—one that herded the suspected mother and another that focused on attacking the neonate. Our study analysed the frequency and variety of behavioural types used in the attack and compared them between individuals and the two separate attack groups. The group change we observed is absent from the literature on conspecific calf-directed attacks in other cetacean species and, if this is an infanticide attempt, provides new insight into the social structure of Pacific white-sided dolphins.

Key Words: aggression, calf harassment, infanticide, social structure, sexual coercion, Pacific white-sided dolphin, *Lagenorhynchus obliquidens*

Introduction

Intraspecific aggression among cetaceans has been reported in multiple different species from the larger baleen whales (e.g., humpback whale [*Megaptera novaeangliae*]; Clapham, 1992) to odontocetes (e.g., *Tursiops* spp.; Östman, 1991; Connor et al., 2000b) and may be attributed to a variety of complex social and sexual factors. In addition to rake marks inflicted during social interactions (McCann, 1974), agonistic behaviour in cetaceans may arise in forms of maternal protection (Mann & Smuts, 1998), dominance between males (Östman, 1991; Samuels & Gifford, 1997), and sexual competition between males (Clapham, 1992; Connor et al., 1992). Most widely reported cases of cetacean aggression are between males. Conspecific male conflict between bottlenose dolphins (*Tursiops aduncus*) has been documented to occur when male alliances compete for and defend consortships with females (Connor et al., 1992, 2000a). Male aggression directed towards the female during sexual coercion is also exhibited in these alliances (Scott et al., 2005).

Dolphin agonistic behaviours range from acoustic threats, jaw-claps, and body posturing to assault (such as ramming, biting, and body slamming) (Herzing, 1996; Connor et al., 2000b; Blomqvist & Amundin, 2004). Physical bodily harm can result in serious injury, from unconsciousness (Parsons et al., 2003a) to death, as seen in recent reports of intraspecific (Towers et al., 2018) and interspecific (Methion & Díaz López, 2021) aggression. While resource competition may play a part in interspecific conflict (Methion & Díaz López, 2021), attacks on smaller cetaceans, such as bottlenose dolphin (*Tursiops truncatus*) attacks on harbour porpoises (*Phocoena phocoena*), may be a method of enhancing physical strength and practicing important fighting skills (Ross & Wilson, 1996; Jepson & Baker, 1998; Patterson et al., 1998; Cotter et al., 2011). Furthermore, dolphin attacks on porpoises may also be a form of "object-play" as was suggested for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Baird, 1998) and white-beaked dolphins (*Lagenorhynchus albirostris*; Haelters & Everaarts, 2011). High testosterone levels in males or male sexual frustration also add to increased aggressive behaviours (Cotter et al., 2011).

The most striking result of intraspecific calf-directed attacks in dolphins is infanticide, or the killing of an infant, a phenomenon documented throughout the animal kingdom in both vertebrate and invertebrate species (Hrdy, 1979). Most reports of cetacean calf-directed aggression and infanticidal behaviour come from the bottlenose dolphin (Patterson et al., 1998; Dunn et al., 2002; Kaplan et al., 2009; Robinson, 2014; Perrtree et al., 2016; Díaz López et al., 2017; Ronje et al., 2020), along with evidence for interspecific infanticide (*T. aduncus*) of a spinner dolphin (*Stenella longirostris*; Estrade & Dulau, 2017). However, infanticidal behaviour has also been uncovered in the Indo-Pacific humpback dolphin (*Sousa chinensis*; Zheng et al., 2016) and the killer whale (*Orcinus orca*; Towers et al., 2018), with further reports of calf-directed attack behaviours in the marine tucuxi dolphin (*Sotalia guianensis*; Nery & Simão, 2009) and Amazon River dolphin (*Inia geoffrensis*; Bowler et al., 2018), as well as reports of "calf-tossing" in dusky dolphins (*Lagenorhynchus obscurus*; Markowitz, 2004). The primary motive suggested for infanticide in odontocetes (e.g., *Tursiops* spp.) is the sexual selection hypothesis in which a male may kill an unrelated calf for the purpose of prematurely ending the mother's lactation period and subsequently bringing her into estrus so that he can mate with her (Hrdy, 1979; Palombit, 2015). It has also been suggested for other mammals with long inter-birth intervals such as lions (*Panthera leo*) and a range of wild primates such as gray langurs (*Presbytis entellus*; Hrdy, 1977) and East African chimpanzees (*Pan troglodytes schweinfurthii*; Lowe et al., 2020).

In this article, we present the first observation of conspecific calf-directed aggression in Pacific white-sided dolphins (proposed to belong to the newly revised *Sagmatias* genus; Vollmer et al., 2019). Within Japanese waters, Pacific white-sided dolphins occur along the Sea of Japan coast and in the North Pacific (Leatherwood et al., 1984; Iwasaki, 1996) wherein genetic differences found between the Japanese Coastal Pacific–Sea of Japan and offshore North Pacific suggest different populations (Hayano et al., 2004). During the months of May and June, large groups on their migratory route northward (Amano, 1998) pass through the Tsugaru Strait, a foraging site (Ono et al., 2010), and enter Mutsu Bay, our study site located in Aomori Prefecture, northern Japan (Iwahara et al., 2017). Pacific white-sided dolphins can be observed in Funka Bay, Hokkaido, from late May to the end of August (Tanaka, 1998). However, there is no evidence to suggest that these groups spotted here are the same that are seen in Mutsu Bay or the Tsugaru Strait (Tsutsui et al., 2001). Pacific white-sided dolphins are seasonal breeders with an approximate gestation length of 10 to 12 months (Ferrero & Walker, 1996). The estimated birthing season for the species in Japan has been suggested from May (Iwasaki & Kasuya, 1997) to July, with lactating females and calves incidentally caught in drift nets around Japanese waters from June to September (Ferrero & Walker, 1996). Neonates are rare within the Tsugaru Strait, and the only suggested birthing site for the species in Japan is Funka Bay in which half of the groups observed in June and July contain small calves with foetal folds (Tanaka, 1998; Ishikawa et al., 2013). Furthermore, reports during this period have also documented stranded neonates with umbilical cords in the area (Ishikawa et al., 2013).

Methods

Since 2016, annual boat-based surveys along the coast of Wakinosawa, located in the northern part of Mutsu Bay, have been carried out using a small fishing vessel as well as opportunistic surveys aboard a sightseeing boat during the months of May and June. Each year, an average of 15 approximately 2-hour surveys are conducted to collect behavioural and photo-identification (ID) data. On 4 June 2020, while surveying near the mouth of the bay, we observed a group of approximately 10 Pacific white-sided dolphins, with significant splashing, close to the coast at a depth of approximately 50 m (41° 10' 55" N, 140° 45' 50" E; Figure 1). The vessel stopped at a distance of 100 m from the dolphins to minimise any disturbance and so as not to impact the behaviour. Beginning at 1156 h, photographs and opportunistic video footage were taken by researchers using a Canon EOS 7D Mark II and 80D with Sigma 100-400 mm and Canon 55-250 mm lens, respectively, following an *ad lib* sampling protocol

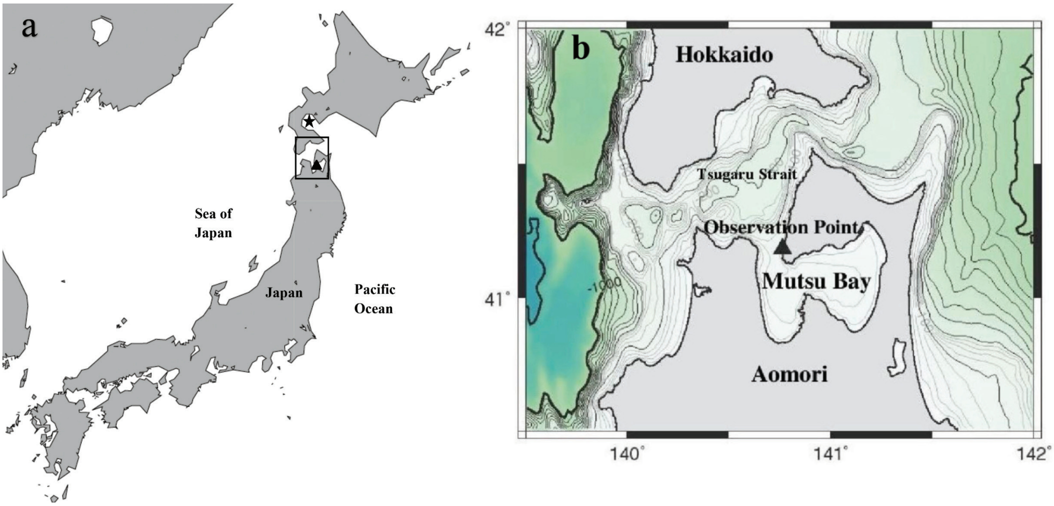

Figure 1. Map of the observation area of Mutsu Bay: (a) location of Mutsu Bay (square) within Japan (triangle indicates Mutsu Bay; star indicates Funka Bay), and (b) detailed map of the squared area in (a) and location of observation point within Mutsu Bay indicated by the triangle.

(Altmann, 1974). Additionally, video footage was continuously recorded with a Go Pro Hero5 (see supplementary video; supplemental materials for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Around 1158 h, it became evident that the dolphin group was already engaged in the attack of a small calf, which was later determined to be a neonate through foetal lines visible in the photographs (Figure 2b).

A timeline of events and behavioural analysis were formulated *post hoc* using the photos and footage taken (along with observational voice notes). Each dolphin was identified by distinguishing unique colouration patterns, dorsal fin notches, and marks (see Supplemental Appendix 1). As our photo-ID study is recent, none of the individuals were known prior, making sex classification difficult due to similarities in body size and dorsal fin shape in mature females and subadult males. However, as dorsal fins are sexually dimorphic, adult males could be distinguished by their large, curved dorsal fins (Kasuya, 2017). These individuals were independently confirmed by six Pacific white-sided dolphin trainers with more than 3 years of experience from five captive facilities in Japan. Each trainer identified which individuals were adult males by evaluating the dorsal fins, and a probability percentage was calculated based on their accumulated verdicts. Individuals were classed as "male" when all six trainers determined the dolphin as male (100% probability), and as "possible male" when the trainers' probability ratings were higher than 80% (when 5 of 6 trainers determined an individual male). We also classified an individual as male if we observed the penis. As the females and subadult males could not be confirmed, the mother of the neonate could only be suggested by apparent displays of protective behaviours, echelon position, and a continued presence with the neonate.

The observation as a whole was referred to as the "attack event." An "attack bout" defines a series of attacking behaviours that start when an attacker first begins to attack and ends with a break in the series such as the neonate escaping. Information recorded *post hoc* included the identification of the attacker(s), along with the number of attack bouts and variety of behaviours used (classified as flip, ram, sandwich, submerge, and bite; Table 1), which were analysed for each attacker.

A timeline was created to record individuals present during 5-minute intervals using a continuous sampling method. If an individual was only recorded for one 5-minute interval, it was considered to be "transient." The attack event was taken over by different individuals at 1250 h, and dolphins were categorised according to this shift into a first group and a second group. The Chi-square goodness of fit test was used to evaluate significant group differences in behavioural types and attack frequency.

Due to boat charter time restrictions, we had to prematurely end the observation; however, we witnessed the attack aggressively continue with no signs of abating as the boat left the area. Nine

Figure 2. Neonate-directed attack with erection visible (black arrows): (a) first group attack and (b) second group attack; neonate foetal lines visible (long arrows), with a rigid fin (short arrow).

additional surveys were conducted throughout June 2020 with no resightings of the neonate or the individuals involved (however, the latter were harder to discern due to the large groups of 100+ individuals often observed).

Results

The neonate, identified as a possible male from photographs of the genital area, remained active throughout the 115 persistent attack bouts (Supplemental Appendix 2), displaying frequent jumps and fleeing attempts. Based on studies of neonate bottlenose dolphins in which dorsal fins become rigid within 2 weeks (McBride & Kritzler, 1951) and foetal folds last from a few months (Cockcroft & Ross, 1990; Mann & Smuts, 1998) to as long as a year (Wilson, 1995), it was estimated that the neonate's age was somewhere within its first year, possibly around 2 months old (Figure 2b).

The neonate had multiple fresh rake marks, some teeth puncture marks, as well as one large, bloody abrasion on the right lateral side (Figure 3) that were all present at the start of the observation. Twenty-four individuals (including the calf) were identified throughout the entire observation, but it is possible that some were missed due to the speed and vigour of the attack.

Sex of the 23 Identified Dolphins (Excluding the Neonate)

Six of the 23 identified dolphins were determined to be male based on the trainers' evaluation (Table 2) of which one individual (#002) had additional confirmation through photographic evidence of an erection. A 7th individual (#018) was also determined to be male by the authors based on an observation of an erection. Two individuals were rated as "possible males" according to a probability percentage higher than 80%. Fourteen of the 23 identified dolphins were of unknown sex, although the identification of the individual regarded as the suspected mother (#004), due to behaviours towards the neonate, was further supported by it being the target of sexual behaviour and coercive guarding by the confirmed and possible male individuals.

Table 1. Descriptions with photos of behaviour types observed within attack bouts

Behaviour	Description
	Attacker propels the neonate, either partially or fully, out of the water by pushing up from underneath, sometimes propelling the neonate vertically.
	A dolphin uses its head, rostrum, or lateral side to strike the neonate with force.
	Two dolphins flank the neonate on either side and squeeze, forcing the neonate to be pushed up or down.
	Attacker pushes the neonate underwater, sometimes holding the neonate down in an attempt to drown it.
	Attacker attempts to bite the neonate.

First Group Attack

During the first group phase, 62 attack bouts occurred. In 25 of these, the attacker could not be identified due to splashing or activity under the surface. There were 16 individuals (including the neonate) present. Of these, the sex could only be confirmed for two males (#002 and #007). Of these individuals, four were observed directly attacking the neonate (#001, #002, #003, and #009). The unfolding of the attack is presented chronologically, based on the photographs and video footage as well as the observers' impressions.

1156 to 1206 h JST—The attack was already underway but difficult to comprehend due to the initial distance. More dolphins approached at speed from the mouth of the bay. To begin with, there were three subgroups: (1) the neonate attack group around 100 m from the vessel, (2) another group approximately 30 m away from the attack, and (3) a third group which could be seen in the distance edging further out of the bay. The movements of the group were erratic, including high-speed surface rushes, with approximately nine individuals either engaged in the attack or involved in chasing behaviours. #004, the possible mother, was mixed tightly in the group or in proximity of the chase and was pursued by transient male #007. The three main attackers (#001, #002, and #003; involved in 92% of identifiable first group attack bouts) persistently chased the neonate, and the first flip was observed in which the neonate was vertically propelled fluke first out of the water. #008 appeared to ram #003 as it pursued the neonate. Similarly, 4 minutes later, #005 pushed down on #006 while chasing the neonate. Further ramming and blocking behaviours

Figure 3. Neonate rake marks and abrasions: (a) bloody abrasion on the right lateral side along with rake marks around the right eye, (b) left lateral side mark, (c) mark on the right ventral side, (d) rake marks close to the genital area, (e) rake marks along the keel and peduncle, and (f) rake marks next to the left eye along with teeth puncture marks.

involving the main attackers occurred, along with seemingly coordinated efforts to sandwich the neonate and submerge it.

1207 to 1215 h JST—The neonate attack subgroup moved further into the bay, pushing the neonate closer to the coast, followed by another subgroup a few minutes later that were surface rushing to join the attack. The subgroups merged into a larger group, with individuals travelling back and forth between the attack and further out of the bay. The neonate, positioned between #005 and #004, was flipped when #009 (involved in 14% of identifiable first group attack bouts) forced itself between the pair. Two previously unseen transient individuals, #012 and #014, surfaced next to the attack, along with #010, who stayed for approximately 20 minutes, and #013.

1222 to 1229 h JST—In a seemingly defensive display, #004 (potential mother) charged #003 as it attempted to bite the neonate. Opportunistic Canon video footage documented a series of synchronized surfaces, with no obvious attacks, every 5 seconds for a total of 50 seconds, with the neonate sandwiched between two attackers, alternating between the three main aggressors.

1230 to 1235 h JST—The attack from this point was mainly performed by the three main aggressors (with #004 still engaged) with no significantly dominant attacker among them (13 to 15 attack bouts). At 1230h, #003 started an attack bout that was finished by #001. The attackers performed a series of strikes during which the neonate was rammed above the surface.

1238 to 1249 h JST—Despite the occasions of coordinated behaviour, photographs revealed attacker #002 ramming #001 and #003. One unidentifiable dolphin blocked another, submerging both of them as the neonate escaped. More dolphins arrived at 1245 h, including #011, who after being sighted at 1158 h had not been present for the last 30 minutes, and male #015 who was seen in pursuit of #004 (the possible mother), after which time sexual behaviour was apparent. #004 attempted to support the neonate at the surface, after which an unidentifiable male charged between the pair belly-up with an erection visible. A male (#002), displaying an erection, used its ventral side to forcefully push the neonate up (Figure 2a). Furthermore, #001 and #003, respectively, were observed ventral side up and dorsal-mounting #004, with the neonate either behind or in echelon position on the other side. #009 flipped the neonate out of the water using its dorsal side, making this the final attack for the first group.

Table 2. Trainers' male probability rating of each identified dolphin

Evaluator	A	B	C	D	E	F	m	
Aquarium	P	Q	Q	R	S	S, T	probability; %	Rating
#001						m	16.7	
#002	m	m	m	m	m	m	100	Male
#003						m	16.7	
#004						m	16.7	
#005						m	16.7	
#006				m	m	m	50.0	
#007	m	m	m	m	m	m	100	Male
#008							0.0	
#009						m	16.7	
#010					m	m	33.3	
#011						m	16.7	
#012						m	16.7	
#013					m	m	33.3	
#014					m	m	33.3	
#015	m	m	m	m	m	m	100	Male
#016	m	m	m	m	m	m	100	Male
#017						m	16.7	
#018						m	16.7	
#019	m	m	m		m	m	83.3	Possible male
#020	m	m	m	m	m	m	100	Male
#021	m	m	m	m	m	m	100	Male
#022	m	m	m			m	66.7	
#023	m	m	m		m	m	83.3	Possible male

Second Group Attack

A previously unrecorded group took over the attack from 1250 h (Table 3). There was a period of overlap where #001 and #003 surfaced with the second group, and a further three individuals involved in the first group (#004, #013, and #015) remained engaged until the end of the observation, making a total of 14 (including the neonate) individuals in the second group. The group contained five males (#015, #016, #018, #020, and #021) and two possible males (#019 and #023). The neonate continued to be persistently chased and attacked with increased aggression by six new attackers (#016, #017, #018, #019, #020, and #022) with no more attacks from the first group. Thirty-six of the 52 attack bouts could be attributed to identifiable individuals.

1250 to 1300 h JST—Male individual #016 (involved in 14% of identifiable second group attack bouts) was the first of the new aggressors to ram and flip the neonate. As with the first group, potential conflict towards the attacker was observed when an individual rammed #022 (involved in 17% of identifiable second group attack bouts) who had the neonate positioned on its back. However, as we could not identify the rammer due to the angle of the dorsal fin, we cannot conclude whether it was another neonate attacker. #022 pushed using its ventral side, thrusting the neonate fluke first above the surface as male individual #018 (involved in 33% of identifiable second group attack bouts) struck towards the head, following which a

Table 3. Timeline of individuals that appear in or close to the neonate attack group during 5-minute intervals

				First group											Second group			
Group	ID	Sex	Note	1155	1200	1205	1210	1215	1220	1225	1230	1235	1240	1245	1250	1255	1300	1305
1st & 2nd	#001	Unknown	Attacker	○	○	○	○	○	○	○	○	○	○	○	○			
1st	#002	Male	Attacker	○	○	○	○	○	○	○	○	○	○	○	○			
1st & 2nd	#003	Unknown	Attacker	○	○	○	○	○	○	○	○	○	○	○	○		○	
1st & 2nd	#004	Unknown	Potential mother	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
1st	#005	Unknown		○	○	○	○	○	○	○	○	○	○	○				
1st	#006	Unknown		○	○	○	○	○	○									
1st	#007	Male	Transient		○													
1st	#008	Unknown			○		○	○										
1st	#009	Unknown	Attacker			○	○	○	○	○	○	○	○	○	○			
1st	#010	Unknown				○	○	○		○								
1st	#011	Unknown		○			○	○						○				
1st	#012	Unknown	Transient					○										
1st & 2nd	#013	Unknown						○	○	○	○	○	○	○	○	○	○	○
1st	#014	Unknown	Transient					○										
1st & 2nd	#015	Male												○	○	○	○	○
2nd	#016	Male	Attacker												○	○	○	○
2nd	#017	Unknown	Attacker												○	○	○	○
2nd	#018	Male	Attacker												○	○	○	○
2nd	#019	Possible male	Attacker												○	○	○	○
2nd	#020	Male	Attacker												○	○	○	○
2nd	#021	Male													○	○	○	○
2nd	#022	Unknown	Attacker												○	○	○	○
2nd	#023	Possible male	Transient													○		

○ = Dolphin recorded during 5-minute interval transient possible male (#023) surfaced next to #015. Distinct subgrouping was often observed throughout the observation—for example, possible male #019 (involved in 11% of identifiable second group attack bouts) and male #021 guarded #004 (the presumed mother) in a sandwich position while a separate subgroup attacked the neonate approximately 5 m away. #017 (involved in 42% of identifiable second group attack bouts), #018, and #019 were consistently in pursuit of the neonate (with #004 close behind) and forced the neonate into a jump before pushing it up from the peduncle. After catching up to the neonate, #022 pushed down on #004, and the three were then blocked by #019. #018 rammed the neonate and flipped it out of the water fluke first. The neonate, once again positioned on the back of the attacker (#022), was flipped fluke first before being pushed down and submerged by #017.

1301 to 1304 h JST—The neonate was rammed and thrown out of the water in a consecutive series of attack bouts by #018 and #017, respectively, after which an unidentifiable attacker appeared to bite the neonate's rostrum. The three main attackers (#017, #018, and #022) cooperatively struck together from multiple angles, hitting the neonate head first up out of the water before thrashing down to submerge it. The neonate was sandwiched between #017 and #022 as #018 propelled its whole body down on the infant. In 2 minutes, the neonate was relentlessly struck 18 times by the main attackers, joined by possible male #019 and males #016 and #020 (involved in 17% of identifiable second group attack bouts). An attacker (#018) lingered belly-to-belly with the neonate, displaying an erection in a seemingly less vigorous moment (Figure 2b).

1305 to 1308 h JST—With a total of seven dolphins in pursuit of the neonate, first group attacker #003 surfaced. #018 rammed #017, and #019 blocked #022 while pressing up next to the neonate positioned close to #004. #019 and #018 guarded #004 with another individual close behind. The neonate was propelled vertically in the air as one individual jumped and dived, while 5 m away #004 was chased in the opposite direction.

Group Patterns

The second group displayed significantly more attack bouts (52 attacks/19 min) than the first group (62 attacks/49 min) (χ^2 (1) = 17.7, p < 0.01). Despite the shorter duration, the second group displayed a significantly greater array of behaviours—focused on submerging, flipping, and sandwiching the neonate—than the first group (χ^2 (1) = 13.5, 28.2, 10.7, p < 0.01, respectively), whereas the first group displayed more ramming

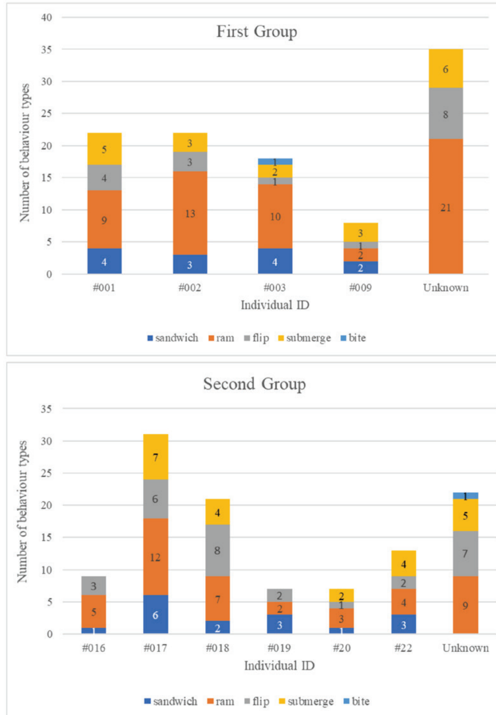

Figure 4. Total number of behaviour types for each attacker in both groups

behaviours (χ^2 (1) = 11.4, p < 0.01). #001 and #017 were both involved in the most attack bouts (15 identifiable bouts), yet #017 displayed more behaviour types (Figure 4). Structurally, the two groups differed in that the second group's subgroups remained approximately 5 to 10 m apart with a frequent transfer of individuals from one to the other, while the first group's subgroups kept further apart to begin with before either joining the attack or possibly leaving the area.

Discussion

Causes behind cetacean aggression are difficult to discern, and the motives of the attackers are most likely a complex combination of factors. Observations of this nature are rare and so our account contributes to the behavioural comprehension of Pacific white-sided dolphins for which data are currently lacking. We explore the following hypotheses to help build an understanding of possible causes that may have provoked this behaviour.

Male Dominance

Along with physical violence, the neonate was also subjected to belly-up attacks in which the aggressor had an erection. Socio-sexual behaviour, typically seen in a less aggressive context and usually serving a social purpose (Mann, 2006), can likely be ruled out due to the intensity of the interaction. The male Indo-Pacific bottlenose dolphins of Shark Bay, Australia, have been seen mounting calves, and male–male mounting with erections has been observed in an agonistic context (Connor et al., 2000b). Furthermore, captive studies of *T. truncatus* have described cases in which sexual behaviour and displays of erections may be gestures of dominance (Caldwell & Caldwell, 1977; Östman, 1991). Therefore, it is plausible that the sexual behaviour directed at the neonate was another form of aggression as a result of the males displaying their dominance.

Object-Oriented Play or Physical Training

The previous report of Pacific white-sided dolphin aggression (an interspecific attack on a harbour porpoise) proposed the interaction to be "object-oriented" play, which may act as physical training for the dolphins (Baird, 1998). Similarly, the "porpicides" witnessed in California (Cotter et al., 2011) and in British waters (Patterson et al., 1998) may allow males to develop important fighting skills by practicing on smaller cetaceans. However, our observation of intraspecific calf-directed aggression also included occasions of larger conspecific conflict directed at the attackers (Möller et al., 2001; Cotter et al., 2011), which have much higher costs. Ramming between attackers (e.g., male #002 ramming #001 and #003) could be an indicator of male–male competitive aggression within the groups that are competing for access to the female (Orbach, 2019).

Male Sexual Frustration

Sexual frustration may occur when experienced males claim access to females over the less experienced males (Le Boeuf & Campagna, 1994). This could have played a part in the "porpicide" in California as the events occurred during mating seasons within years of low female availability, as well as a skewed male–female ratio within the Monterey Bay bottlenose dolphin population (Cotter et al., 2011). Although the population sex ratio is unknown in Japan's Pacific white-sided dolphins, certain factors play into the possibility of limited numbers of sexually receptive females. First, unlike bottlenose dolphins, male and female Pacific white-sided dolphins exhibit a distinct ~3 month reproductive seasonality (Ferrero & Walker, 1996; Robeck et al., 2009; Ashe, 2015). Females also have a lengthy 4.2- to 4.5-year inter-birth interval (Taylor et al., 2007; Ashe, 2015) further restricting male access to females. Given that the gestation period is 10 to 12 months (Ferrero & Walker, 1996) and calves are seen in Japan from May (Iwasaki & Kasuya, 1997), this attack occurred during a possible mating period and, thus, the sexual frustration of the less-experienced males could be another contributing factor.

Heightened Testosterone Levels

Both captive and wild-caught Pacific white-sided dolphin hormone sampling has shown heightened levels of testosterone in males during May and June (Yoshioka, 1996), with peak levels reached in July (Robeck et al., 2009). High testosterone levels often enable increased aggression to coincide with periods of reproductive competition and have been linked to heightened aggression in males for several vertebrate species (Archer, 1988; Cotter et al., 2011). As our observation took place during this period of increased testosterone levels, as well as during a possible mating period, this may have contributed to the male dolphin aggression we witnessed.

Sexually Selected Infanticide Attempt

The sexual selection hypothesis in which a male will kill an unrelated infant to make the mother sexually receptive again has been suggested as the primary motive behind infanticide in dolphins (Palombit, 2015). Sexual behaviour directed at #004 (the possible mother) was witnessed in both groups, including mounting, intromission attempts, and coercive guarding, along with forceful attempts to maintain separation between the mother–calf pair using a subgrouping tactic. The suspected mother in our observation may have been a non-cycling female due to the presence of the neonate, which could suggest that the herding we observed was the attackers' attempt to kill the infant to make the female sexually receptive again. Female bottlenose dolphins who have lost offspring can conceive again within the same season (Mann et al., 2000), even becoming sexually receptive within 7 to 11 days of losing a calf (Connor et al., 1996). Although this tactic would be an effective strategy to increase male reproductive fitness in limited populations, the probability of these attackers remaining with this female until she is sexually receptive after the loss of her calf might be relatively low. Pacific white-sided dolphins belong to large, wide-ranging populations often observed in groups of 100+ individuals. It is believed that they follow annual migration patterns around a large area (Amano, 1998). Furthermore, it is not uncommon for dolphins to ovulate while lactating (Whitehead & Mann, 2000; West et al., 2007). One study of the Shark Bay dolphins found that male to female aggression was predominantly targeted at cycling females (Scott et al., 2005), so, alternatively, it could be possible that the female was exhibiting some attractive hormonal state to the males which induced sexual arousal and provoked such energetically costly aggressive behaviour towards the calf. This raised the possibility of our observation being a mating attempt with an estrus female in which the neonate may have been preventing the males from achieving copulation.

Vulnerability of Location and Small Group Size
Although our data is limited to the Wakinosawa coast, this is our first sighting of a neonate during 5 years of surveying. As neonates are usually spotted in Funka Bay (Figure 1a) in late June to July (Ishikawa et al., 2013), it is possible that the location away from the relative safety of a birthing site potentially left the neonate exposed to harassment. Although some seemingly non-aggressive individuals displayed possible support by attacking the attackers early on (e.g., #008 rammed #003), the mother–calf pair were predominantly left to fend for themselves making them vulnerable to danger. The formation of mother–calf nurseries may partly act as a protective tool against male harassment and infanticide (Connor et al., 1996, 2000b; Connor, 2000). In addition to bottlenose dolphins, dusky dolphins, close relatives of Pacific white-sided dolphins, also use this tactic to avoid conspecific male aggression towards calves (Weir et al., 2008). Furthermore, male aggressive sexual behaviour towards lactating females is a common reason for separation of the sexes in captivity (Caldwell & Caldwell, 1977). Pacific white-sided dolphins usually travel in large groups in which calves may be more difficult to spot due to the vast number of individuals. Additional protection may also come from the "dilution effect" (Foster & Treherne, 1981, pp. 466-467) in which mother–calf pairs can conceal themselves within less-exposed positions of the group (i.e., the centre) (Ashe, 2015).

Other Notable Points Regarding Group Change
The most significant difference from other accounts of cetacean calf-directed aggression is the distinct group change between attackers. There was no evidence of a physical conflict between the two groups, yet the second group seized control with no further attempts from the first group to attack the neonate, a suggestion of submissive behaviour that could indicate second group dominance (Samuels & Gifford, 1997). Statistical analysis conducted in this study supports second group dominance showing that the second group displayed significantly more attack bouts, using a wider range of behaviour types. The second group continued the attack with more intensity and succeeded in stealing and herding the female away from the first group attackers without any apparent contest. In our observation, the larger and seemingly more dominant second group took over the herding of the suspected mother and formed distinct subgroups to cooperatively remove the neonate while simultaneously guarding the female. This effort is energetically very costly and so the second group would need to benefit, further hinting at this behaviour being a male reproductive strategy. Although the social structure of Pacific white-sided dolphins is relatively understudied, male testes size relative to their body mass is smaller than expected, making it likely that the species favours pre-copulatory competition in which males monopolise females (Connor, 2000).

As this is the first observation of a group takeover during a calf-directed attack, it is difficult to assess the reasons for the switch. Perhaps the group takeover was an act of cooperation after the first group had used up their energy reserves. There was a brief merging of the groups when some members of the first group surfaced with the second, and it is possible that the second group was part of the initial first group that travelled further out of the bay. Male long-term social bonds have been suggested within the Pacific white-sided dolphins in British Columbia, Canada (Ashe, 2015). Similarly, studies in New Zealand of the closely related dusky dolphin have also indicated possible cooperative male alliances in which some males will feed together in the same foraging area as well as chase females together in a different location during the breeding season (Markowitz, 2004; Markowitz et al., 2010). Little sexual dimorphism exists in Pacific white-sided dolphins and, due to their long inter-birth intervals (Taylor et al., 2007; Ashe, 2015), receptive females are limited. Both of these factors generally allow for the formation of male alliances (Möller et al., 2001; Parsons et al., 2003b; Whitehead & Connor, 2005); however, much more behavioural and social data on the Pacific white-sided dolphin are needed to better understand male social bonds.

Epimeletic Behaviour
The multiple fresh rake marks and abrasions over the neonate's body are indicative of aggressive behaviours using the teeth. The rake marks along the peduncle suggest the neonate was held in an individual's mouth, possibly as an act of aggression, or it could indicate succorant behaviour (Norris & Prescott, 1961; Connor & Norris, 1982) from the proposed mother, dragging her distressed calf away from danger (although neither were observed due to the speed of the event).

Therefore, rake marks along the calf's peduncle, combined with evidence of the proposed mother supporting her calf at the surface and continued attempts to rejoin the neonate by forming the echelon position, further support the possibility of epimeletic behaviour at the site. Further protective behaviours towards the calf are suggested by the observed ramming between non-attacking individuals—for example, smaller individual #008 rammed attacker #003, who was chasing the neonate, which was a risky attempt to intervene and defend the calf. During the coercive guarding, the suspected mother persistently made attempts to rejoin the neonate, surface rushing between subgroups, but was often corralled away from her calf. These continued efforts to retrieve the neonate from the attackers may be a reason why after 75 minutes of 115 attack bouts the death of the neonate was still not observed. A case in Scotland documents a bottlenose dolphin calf that died 7 months after an aggressive male attack due to acute scoliosis caused by the blunt trauma sustained from the incident (Robinson, 2014). In addition to the external damage, the more serious aggression (Connor et al., 2000b), such as the flips and rams we observed, often cause injuries that prove to be fatal (Jepson & Baker, 1998), suggesting that our limited survey time was the only reason why we didn't observe the death.

Conclusion

Although the causes of cetacean aggression are difficult to discern, the extensive and persistent calf-directed aggressive behaviours we observed are consistent with reports of cetacean infanticidal behaviour (Kaplan et al., 2009; Robinson, 2014; Perrtree et al., 2016; Zheng et al., 2016; Díaz López et al., 2017; Towers et al., 2018). Even though in this case we cannot confirm the death of the neonate, we believe the execution and tenacity of the attack along with the attackers' continual efforts to keep the suspected mother separated from her calf demonstrate an intent to kill. We suggest that the repeated mating attempts, whether the presumed mother was in estrus or not, indicate that the calf-directed attack was the result of the males' reproductive strategy to mate with her. We also believe that the vulnerability of location and group size were a contributing factor. Necropsy studies of stranded Pacific white-sided dolphin calves around Japan that could confirm infanticide as the cause of death, as has been reported in other infant cetacean species (Ross & Wilson, 1996; Patterson et al., 1998; Dunn et al., 2002; Zheng et al., 2016; Estrade & Dulau, 2017), could support our observation as a possible infanticide attempt and help shed further light on the behaviour in this species. Further long-term individual and sex identification studies in this species are needed to assess group structure and population sex ratio.

Acknowledgements

We are grateful to Captain Kunihiro Tanaka for his skillful guidance on our boat surveys and to research assistant Daniel Rosser for his photography during this observation. Special thanks to the reviewers for helping to improve this manuscript. We would also like to thank Megumi Ishikawa, Teruyo Matsumoto, Shuhei Nishimoto, Mahiro Ryono, Ryo Takehana, and Saki Yamaguchi for helping us to identify the sex of the dolphins. This research was supported by the Museum of Maritime Science's Uminomanabi Museum Support Programme 2A 2019.

Literature Cited

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267. https://doi.org/10.1163/156853974X00534

Amano, M. (1998). 黒潮・親潮移行域における小型ハクジラ類の分布と回遊 [The distribution and migration of small odontocetes in the Kuroshio-Oyashio transition region]. *Kaiyo Extra*, *13*, 187-191.

Archer, J. (1988). *The behavioral biology of aggression: Cambridge studies in behavioral biology*. Cambridge University Press.

Ashe, E. (2015). *Ecology of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the coastal waters of British Columbia, Canada* (Doctoral thesis). University of St Andrews, St Andrews, Scotland. https://research-repository.st-andrews.ac.uk/bitstream/handle/10023/9483/ErinAshePhDThesis.pdf?sequence=2&isAllowed=y

Baird, R. W. (1998). An interaction between Pacific white-sided dolphins and a neonatal harbour porpoise. *Mammalia*, *62*(1), 129-133.

Blomqvist, C., & Amundin, M. (2004). High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In J. A. Thomas, C. Moss, & M. Vater (Eds.), *Echolocation in bats and dolphins* (pp. 425-430). University of Chicago Press.

Bowler, M. T., Griffiths, B. M., Gilmore, M. P., Wingfield, A., & Recharte, M. (2018). Potentially infanticidal behaviour in the Amazon river dolphin (*Inia geoffrensis*). *Acta Ethologica*, *21*, 141-145. https://doi.org/10.1007/s10211-018-0290-y

Caldwell, D. K., & Caldwell, M. C. (1977). Cetaceans. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 794-808). Indiana University Press.

Clapham, P. J. (1992). The attainment of sexual maturity in humpback whales. *Canadian Journal of Zoology*, *70*, 1470-1472. https://doi.org/10.1139/z92-202

Cockcroft, V., & Ross, G. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 461-478). Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50031-7

Connor, R. C. (2000). Group living in whales and dolphins. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199-218). University of Chicago Press.

Connor, R. C., & Norris, K. S. (1982). Are dolphins reciprocal altruists? *The American Naturalist*, *119*(3), 358-374. https://doi.org/10.1086/283915

Connor, R. C., Read, A. J., & Wrangham, R. (2000a). Male reproductive strategies and social bonds. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 247-269). University of Chicago Press.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, *89*(3), 987-990. https://doi.org/10.1086/283915

Connor, R. C., Richards, A. F., Smolker, R. A., & Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*, *133*(1/2), 37-69. https://doi.org/10.1163/156853996X00026

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000b). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199-218). University of Chicago Press.

Cotter, M. P., Maldini, D., & Jefferson, T. A. (2011). "Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *28*(1), E1-E15. https://doi.org/10.1111/j.1748-7692.2011.00474.x

Díaz López, B., López, A., Methion, S., & Covelo, P. (2017). Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*). *Journal of the Marine Biological Association of the United Kingdom*, *98*, 1-9. https://doi.org/10.1017/S0025315417001266

Dunn, D., Barco, S., Pabst, D., & McLellan, W. (2002). Evidence for infanticide in bottlenose dolphins of the western North Atlantic. *Journal of Wildlife Diseases*, *38*, 505-510. https://doi.org/10.7589/0090-3558-38.3.505

Estrade, V., & Dulau, V. (2017). First case of spinner dolphin (*Stenella longirostris*) infanticide off Reunion Island: Necropsy's findings and post mortem interspecies interactions. *Oceanography & Fisheries Open Access Journal*, *3*(3), 555615. https://doi.org/10.19080/OFOAJ.2017.03.555615

Ferrero, R. C., & Walker, W. A. (1996). Age, growth, and reproductive patterns of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) taken in high seas drift nets in the central North Pacific Ocean. *Canadian Journal of Zoology*, *74*, 1673-1687. https://doi.org/10.1139/z96-185

Foster, W., & Treherne, J. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, *293*, 466-467. https://doi.org/10.1038/293466a0

Haelters, J., & Everaarts, E. (2011). Two cases of physical interaction between white-beaked dolphins (*Lagenorhynchus albirostris*) and juvenile harbour porpoises (*Phocoena phocoena*) in the southern North Sea. *Aquatic Mammals*, *37*(2), 198-201. https://doi.org/10.1578/AM.37.2.2011.198

Hausfater, G., & Hrdy, S. B. (Eds.). (1984). *Infanticide: Comparative and evolutionary perspectives*. Aldine Publishing. https://doi.org/10.1086/203169

Hayano, A., Yoshioka, M., Tanaka, M., & Amano, M. (2004). Population differentiation in the Pacific white-sided dolphin *Lagenorhynchus obliquidens* inferred from mitochondrial DNA and microsatellite analyses. *Zoological Science*, *21*, 989-999. https://doi.org/10.2108/zsj.21.989

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, *22*(2), 61-79.

Hrdy, S. B. (1977). Infanticide as a primate reproductive strategy: Conflict is basic to all creatures that reproduce sexually, because the genotypes, and hence self-interests, of consorts are necessarily nonidentical. Infanticide among langurs illustrates an extreme form of this conflict. *American Scientist*, *65*(1), 40-49. www.jstor.org/stable/27847641

Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13-40. https://doi.org/10.1016/0162-3095(79)90004-9

Ishikawa, H., Goto, M., & Mogoe, T. (2013). 下関鯨類研究室報告： 日本沿岸のストランディングレコード (1901-2012) No. 1 [Reports of whale laboratory in Shimonoseki No. 1: Stranding record in Japan (1901-2012)]. Shimonoseki Academy of Marine Science.

Iwahara, Y., Mitani, Y., & Miyashita, K. (2017). Estimation of environmental factors that influence migration timing and distribution of Pacific white-sided dolphins around Hokkaido, Japan. *Pacific Science*, *71*, 303-318. https://doi.org/10.2984/71.3.5

Iwasaki, T. (1996). Pacific white-sided dolphin. In K. Izawa, T. Kasuya, & T. Kawamichi (Eds.), *Encyclopedia of animals in Japan* (Vol. 2, pp. 70-71). Heibonsha Limited.

Iwasaki, T., & Kasuya, T. (1997). Life history and catch bias of Pacific white-sided (*Lagenorhynchus obliquidens*) and northern right whale dolphins (*Lissodelphis borealis*) incidentally taken by the Japanese high seas squid driftnet fishery. *Reports of the International Whaling Commission*, *47*, 683-692.

Jepson, P. D., & Baker, J. R. (1998). Bottlenose dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Veterinary*

Record, *143*(22), 614-615. https://doi.org/10.1136/vr.143.22.614

Kaplan, J., Lentell, B., & Lange, W. (2009). Possible evidence for infanticide among bottlenose dolphins (*Tursiops truncatus*) off St. Augustine, Florida. *Marine Mammal Science*, *25*(4), 970-975. https://doi.org/10.1111/j.1748-7692.2009.00323.x

Kasuya, T. (2017). *Small cetaceans of Japan: Exploitation and biology* (W. F. Perrin, Ed.). CRC Press. https://doi.org/10.1201/b21801

Leatherwood, S., Reeves, R. R., Bowles, A. E., Stewart, B. S., & Goodrich, K. R. (1984). Distribution, seasonal movements, and abundance of Pacific white-sided dolphins in the eastern North Pacific. *Scientific Reports of the Whales Research Institute*, *35*, 129-157.

Le Boeuf, B. J., & Campagna, C. (1994). Protection and abuse of young in pinnipeds. In S. Parmigiani & F. Vom Saal (Eds.), *Infanticide and parental care* (pp. 257-276). Routledge.

Lowe, A. E., Hobaiter, C., Asiimwe, C., Zuberbühler, K., & Newton-Fisher, N. E. (2020). Intra-community infanticide in wild, eastern chimpanzees: A 24-year review. *Primates*, *61*, 69-82. https://doi.org/10.1007/s10329-019-00730-3

Mann, J. (2006). Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In V. Sommer & P. L. Vasey (Eds.), *Homosexual behaviour in animals: An evolutionary perspective* (pp. 107-130). Cambridge University Press.

Mann, J., & Smuts, B. (1998). Natal attraction: Allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour*, *55*, 1097-1113. https://doi.org/10.1006/anbe.1997.0637

Mann, J., Connor, R., Barre, L., & Heithaus, M. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*(2), 210-219. https://doi.org/10.1093/beheco/11.2.210

Markowitz, T. M. (2004). *Social organization of the New Zealand dusky dolphin* (Doctoral thesis). Texas A&M University, Galveston, Texas. https://core.ac.uk/download/pdf/147123046.pdf

Markowitz, T. M., Markowitz, W. J., & Morton, L. M. (2010). Mating habits of New Zealand dusky dolphins. In B. Würsig & M. Würsig (Eds.), *The dusky dolphin: Master acrobat off different shores* (pp. 151-176). Academic Press/Elsevier. https://doi.org/10.1016/B978-0-12-373723-6.00008-4

McBride, A. F., & Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, *32*(3), 251-266. https://doi.org/10.2307/1375657

McCann, C. (1974). Body scarring on Cetacea – odontocetes. *Scientific Reports of the Whale Research Institute Tokyo*, *26*, 145-155.

Methion, S., & Díaz López, B. (2021). Spatial segregation and interspecific killing of common dolphins (*Delphinus delphis*) by bottlenose dolphins (*Tursiops truncatus*). *Acta Ethologica*, *24*(3). https://doi.org/10.1007/s10211-021-00363-0

Möller, L. M., Beheregaray, L. B., Harcourt, R. G., & Krützen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*, 1941-1947. https://doi.org/10.1098/rspb.2001.1756

Nery, M. F., & Simão, S. M. (2009). Sexual coercion and aggression towards a newborn calf of marine tucuxi dolphins (*Sotalia guianensis*). *Marine Mammal Science*, *25*, 450-454. https://doi.org/10.1111/j.1748-7692.2008.00275.x

Norris, K. S., & Prescott, J. H. (1961). Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, *63*, 291-402.

Ono, Y., Sahashi, G., Nishizawa, B., Yamada, W., Shibata, Y., & Matsuishi, T. (2010). 津軽海峡におけるカマイルカ群れサイズの時間的変動 [Temporal change of school size in Pacific white-sided dolphin *Lagenorhynchus obliquidens* in the Tsugaru Strait, Japan]. *Japan Cetology*, *20*, 13-15. https://doi.org/10.5181/cetology.0.20_13

Orbach, D. N. (2019). Sexual strategies: Male and female mating tactics. In B. Würsig (Ed.), *Ethology and behavioural ecology of odontocetes* (pp. 75-93). Springer. https://doi.org/10.1007/978-3-030-16663-2_4

Östman, J. (1991). Changes in aggressive and sexual behavior between two male bottlenose dolphins (*Tursiops truncatus*) in a captive colony. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 305-317). University of California Press.

Palombit, R. (2015). Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology*, *7*(6), a017640. https://doi.org/10.1101/cshperspect.a017640.

Parsons, K. M., Durban, J. W., & Claridge, D. E. (2003a). Male-male aggression renders bottlenose dolphin (*Tursiops truncatus*) unconscious. *Aquatic Mammals*, *29*(3), 360-362.

Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. R., & Thompson, P. M. (2003b). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, *66*, 185-194. https://doi.org/10.1006/anbe.2003.2186

Patterson, I., Reid, R., Wilson, B., Grellier, K., Ross, H., & Thompson, P. (1998). Evidence for infanticide in bottlenose dolphins: An explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society B: Biological Sciences*, *265*, 1167-1170. https://doi.org/10.1098/rspb.1998.0414

Perrtree, R., Sayigh, L., Williford, A., Bocconcelli, A., Curran, M., & Cox, T. (2016). First observed wild birth and acoustic record of a possible infanticide attempt on a common bottlenose dolphin (*Tursiops truncatus*). *Marine Mammal Science*, *32*(1), 376-385. https://doi.org/10.1111/mms.12248

Robeck, T. R., Steinman, K. J., Greenwell, M., Ramirez, K., Van Bonn, W., Yoshioka, M., Katsumata, E., Dalton, L., Osborn, S., & O'Brien, J. K. (2009). Seasonality, estrous cycle characterization, estrus synchronization, semen cryopreservation, and artificial insemination in the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). *Reproduction*, *138*, 391-405. https://doi.org/10.1530/REP-08-0528

Robinson, K. (2014). Agonistic intraspecific behavior in free-ranging bottlenose dolphins: Calf-directed aggression and infanticidal tendencies by adult males. *Marine Mammal Science*, *30*(1), 381-388. https://doi.org/10.1111/mms.12023

Ronje, E., Piwetz, S., Whitehead, H., & Mullin, K. D. (2020). Intraspecific aggression towards common bottlenose dolphin calves, northern Gulf of Mexico. *Gulf and Caribbean Research*, *31*(1), SC6-SC12. https://doi.org/10.18785/gcr.3101.07

Ross, H. M., & Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society B: Biological Sciences*, *263*, 283-286. https://doi.org/10.1098/rspb.1996.0043

Samuels, A., & Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science*, *13*, 70-99. https://doi.org/10.1111/j.1748-7692.1997.tb00613.x

Scott, E., Mann, J., Watson-Capps, J., Sargeant, B., & Connor, R. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, *142*, 21-44. https://doi.org/10.1163/1568539053627712

Tanaka, M. (1998). 室蘭沖に来遊するカマイルカ群の生態学的研究 [Biological study on Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) off Muroran, Hokkaido, Japan] (Master's thesis). University of Tokyo, Tokyo, Japan.

Taylor, B. L., Chivers, S. J., Larese, J., & Perrin, W. F. (2007). *Generation length and percent mature estimates for IUCN assessments of cetaceans* (Administrative Report LJ-07-01). Southwest Fisheries Science Center. 24 pp.

Towers, J., Hallé, M., Symonds, H., Sutton, G., Morton, A., Spong, P., Borrowman, J., & Ford, J. (2018). Infanticide in a mammal-eating killer whale population. *Scientific Reports*, *8*, 4366. https://doi.org/10.1038/s41598-018-22714-x

Tsutsui, S., Tanaka, M., Miyazaki, N., & Furuya, T. (2001). Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) with anomalous colour patterns in Volcano Bay, Hokkaido, Japan. *Aquatic Mammals*, *27*(2), 172-182.

Vollmer, N. L., Ashe, E., Brownell, R. L., Jr., Cipriano, F., Mead, J. G., Reeves, R. R., Soldevilla, M. S., & Williams, R. (2019). Taxonomic revision of the dolphin genus *Lagenorhynchus*. *Marine Mammal Science*, *35*(3), 957-1057. https://doi.org/10.1111/mms.12573

Weir, J. S., Duprey, N. M. T., & Würsig, B. (2008). Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: Are shallow waters a refuge for nursery groups? *Canadian Journal of Zoology*, *86*(11), 1225-1234. https://doi.org/10.1139/Z08-101

West, K. L., Oftedal, O. T., Carpenter, J. R., Krames, B. J., Campbell, M., & Sweeney, J. C. (2007). Effect of lactation stage and concurrent pregnancy on milk composition in the bottlenose dolphin. *Journal of Zoology*, *273*(2), 148-160. https://doi.org/10.1111/j.1469-7998.2007.00309.x

Whitehead, H., & Connor, R. C. (2005). Alliances I: How large should alliances be? *Animal Behaviour*, *69*, 117-126. https://doi.org/10.1016/j.anbehav.2004.02.021

Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans: Life histories and calf care. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 219-246). University of Chicago Press.

Wilson, B. (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species' range* (Doctoral thesis). University of Aberdeen, Aberdeen, UK.

Yoshioka, M. (1996). 鯨類の繁殖生理学 (総説) [Reproductive physiology in cetaceans (Review)]. *The Bulletin of the Faculty of Bioresources* (Mie University, Mie, Japan), *16*, 45-48.

Zheng, R., Karczmarski, L., Lin, W., Chan, S. C. Y., Chang, W., & Wu, Y. (2016). Infanticide in the Indo-Pacific humpback dolphin (*Sousa chinensis*). *Journal of Ethology*, *34*(3), 299-307. https://doi.org/10.1007/s10164-016-0475-7