Behavioural responses of migrating humpback whales to swim-with-whale activities in the Ningaloo Marine Park, Western Australia

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ABSTRACT

Swim-with-whale tourism is a lucrative and rapidly growing industry worldwide. Whale-watching can cause negative effects on the behaviour of targeted animals. Although this is believed to be particularly true for close-up interactions, such as swim-with operations, few empirical studies have investigated this. In 2016, the Western Australian State Government commenced a swim-with humpback whale (M. novaeangliae) trial in the Ningaloo Marine Park, where 11 commercial licences were granted. The swim-with trial was conducted during both the northern and southern whale migration (August to November), during which we assessed potential short-term behavioural effects on humpback whales to swim-with activities. From both an independent research vessel (n = 300 h) and on-board commercial swim-with vessels (n = 357 h), we collected group-follow data (n = 224) on whale behaviour before, during and after swim-with activities. Behavioural effects on whales were investigated, including movement patterns (deviation and directness index, heading, swim speed), surfacing patterns (dive duration and respiration rate) and occurrence of agonistic behaviours. Results showed that the most common type of vessel approach to place swimmers in the water was in the path of whales (89.8% of interactions). During in-path approaches, vessels travelled significantly faster (P = .002) compared to when approaching from the side (side-line abreast approaches). When vessels approached in the whales’ path, whales exhibited horizontal and vertical avoidance strategies by adopting a less predictable path (deviating from 32° to 46°), increasing turning angles away from the vessel (heading from 73° to > 90°), increasing swim speeds (from 1.68 to 1.89 ms⁻¹), and decreasing the duration of their dives (from 224 to 194 s). Whales displayed a higher frequency of agonistic behaviours when a swim-with vessel was < 100 m distance from them compared to > 100 m away (P = .011). Young-of-year calves were present during 19.6% (18 of 92) of group-follows that included swim attempts. To reduce potential impacts on whales and increase swimmer safety, we recommend to avoid in-path vessel approaches, not place swimmers in the water with groups of whales that perform agonistic behaviours, and avoid swimming with young-of-year calves.

1. Introduction

Swimming with free-ranging cetaceans is increasing in popularity globally (Hoyt, 2018). Swim-with-whale tourism occurs in numerous countries, in both tropical and temperate waters (for reviews see Hendrix and Rose, 2014; Rose et al., 2005; Samuels et al., 2003). For large whales, the most common species for swim-with-whale tourism is the humpback whale (M. novaeangliae), which is popular to swim with because of its cosmopolitan and near-coastal distribution. Swim-with-whale tourism differs from regular boat-based whale-watching, in that the boat generally positions itself closer to the cetaceans, facilitating swimmers to enter the water to observe the animals underwater (Lundquist et al., 2013).

For boat-based whale-watching, several studies have reported short-term behavioural effects on cetaceans. These include alterations of dive patterns, swim speeds, orientation, group cohesiveness, behavioural state and changes in whale acoustic behaviour (for reviews see Bejder and Samuels, 2003; Higham et al., 2014; Senigaglia et al., 2016). These
effects may be influenced by factors such as the approach tactic of the tour operators and the duration of the interaction, the animals’ group composition and behavioural state, and the surrounding environment (Christiansen and Lusseau, 2014). Short-term effects on baleen whales vary among species, location and whether the location is a foraging ground, breeding ground or migration corridor (Bain et al., 2014; Senigaglia et al., 2016). For example, minke whales (*Balaenoptera acutorostrata*) on their feeding ground off Iceland increase their respiration rates (Christiansen et al., 2014), perform shorter dives and increase sinus movements in the presence of whale-watching vessels (Christiansen et al., 2013). Humpback whales on their breeding grounds off Ecuador and New Caledonia react by significantly increasing their swim speed (Scheidat et al., 2004) and decreasing their path predictability (Schaffar et al., 2013).

The swim-with-whale industry is largely understudied, and there is limited information available on the potential short-term effects on baleen whales (Gero et al., 2016; Machernis et al., 2018). Studies available from Península Valdés, Argentina, documented that southern right whales (*Eubalaena australis*) on their breeding ground decreased their time resting and increased their time travelling by 22% (Lundquist et al., 2008), with mothers and calves being the most sensitive to swim-with activities (Lundquist et al., 2013). Other studies conducted on the humpback whale breeding grounds off the Kingdom of Tonga documented that whales departed from swimmers more quickly if swimmers were loud and surface active, that closer approaches of vessels increased the whales’ activity level (Kessler et al., 2013) and that respirations of mother and calves increased three-fold in the presence of the boat and swimmers (Fiori et al., 2019). Overall, swim-with activities may cause more disturbance to cetaceans than regular boat-based whale-watching due to close vessel approaches and encounters (Lundquist et al., 2008; Vermeulen et al., 2012), and simultaneously pose a greater risk of injury to human swimmers due to the close proximity to large, unpredictable whales (Commonwealth of Australia, 2017; Samuels et al., 2000; Sprogis et al., 2017).

In Australia, swim-with tourism with baleen whales began off the Great Barrier Reef, Queensland, in 1996 with dwarf minke whales (Birles et al., 2002; Valentine et al., 2004), and then after 2013 off Queensland (Mooloolaba, Hervey Bay) and New South Wales (Coffs Harbour, Jervis Bay) with humpback whales. In 2016, the Western Australian State Government commenced a trial for in-water humpback whale activities (*herein* ‘swim-with’) in the Ningaloo Marine Park, Western Australia (WA), where 11 commercial licences were granted (Department of Parks and Wildlife, 2017). Due to a lack of knowledge about the potential impact of swim-with humpback whale tourism in Australia, research was commissioned by the WA Department of Parks and Wildlife¹ (Irvine and Salgado Kent, 2017; Rodger et al., 2017; Sprogis et al., 2017). In this paper, we investigate the potential short-term behavioural effects on humpback whales to swim-with activities.

2. Methods

2.1. Study site and species

The study was conducted between 1 August and 12 October 2016 in the Ningaloo Marine Park, WA (Fig. 1). The marine park was accessed from Coral Bay, Tantabiddi, Bundegi and Exmouth Marina (Fig. 1). The WA humpback whale population (*Antarctica breeding stock D*) migrates along the western Australian coast line between May and December, passing through the marine park on both their northern and southern migratory routes, with peak numbers in July and mid-September (Jenner et al., 2001). Ningaloo Reef provides an important migratory corridor for humpback whales, including mothers and their newborn calves (Irvine et al., 2018). This population is currently estimated at > 30,000 whales and has been increasing 9.7–13% per annum (Bejder et al., 2016; Salgado Kent et al., 2012).

2.2. Swim-with operators and regulations

During the swim-with trial, the WA State government granted 11 licences to tour operators to swim-with humpback whales. This study focused on the nine tour operators that engaged in swim-with humpback whale activities frequently enough to evaluate potential impacts. Of these, two vessels operated from Exmouth Marina, five from Tantabiddi and two from Coral Bay (Fig. 1). Vessels ranged from 12.19 to 21.90 m in length. One was a catamaran, whilst the other vessels were rigid hulled with engines ranging from 450 to 750 hp. Tours began around mid-morning and lasted on average 6.5 h (including a pre-swim snorkel test).

Operators used a spotter aircraft to locate whale groups, identify whales likely to provide a successful swim-with interaction (e.g. not constantly deep diving), and direct swim-with vessels to the whales.

For the swim-with humpback whale trial, the following licence conditions for the tour operators were developed by the Department of Parks and Wildlife (2016);

i) Licensed vessels could only enter the Exclusive Contact Zones (ECZ) when conducting swim-with interactions (ECZ = 50–100 m from the side of whale, or > 150 m in front of whale (Supplementary material 1),

ii) Only one licensed vessel permitted within the ECZ at any one time, and may enter the ECZ a maximum of three times (i.e. several swim attempts can be made) and for no longer than 60 min collectively,

iii) A maximum of seven people (including two crew members; swim guide and photographer) from one licensed vessel allowed in the water with a whale at any one time. The licensee shall ensure that swimmers (including staff) do not approach closer than 30 m from any humpback whale,

iv) No swimming with calves or with groups containing calves.

See Department of Parks and Wildlife (2017) and Sprogis et al. (2017) for further licence conditions.

The definition of what constituted a ‘calf’ provided by the Department of Parks and Wildlife changed during the season. Initially, a calf was defined as “a young whale, approximately half the length or less of adult individuals of its species”. This definition did not preclude interactions with all young-of-year calves, as young-of-year calves in Exmouth Gulf can grow > 50% of their mother’s length (Christiansen et al., 2016; Sprogis et al., 2017). The Department of Parks and Wildlife revised the definition of ‘calf’ on 23 September 2016 to “a young whale, paler in colour than adults of its species and/or less than 8 metres in length and/or less than two thirds of the length of the adult it is in association with” to capture the larger calves later in the breeding season. The definition of a ‘calf’ by the Department was then reverted to its original definition on 8 October 2016.

2.3. Field data collection

A research vessel (6.1 m rigid hull, 140 hp) was used to conduct humpback whale focal follows (hereafter referred to as follows) (for details see Sprogis et al., 2017). Data were collected using a group-follow protocol (Mann, 1999) as individuals within a group could not readily be identified during each surfacing. A group was defined as individuals within 100 m of each other, moving in the same general direction and coordinating their behaviours (Whitehead, 1983). Global positioning system (GPS) recorded the position of the research vessel at one-second intervals. A follow commenced once a whale(s) had been sighted and the research vessel was sufficiently close to collect data (~200 m). At the beginning of a follow, group size, composition, activity state (resting, travelling, milling, socialising; Supplementary

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¹ Currently named Department of Biodiversity, Conservation and Attractions.
Material 2) and Beaufort sea state were recorded. Group composition categories were classified as groups with or without calves. A calf was defined as an animal born during the current breeding season, and was identified based on two attributes: i) an animal consistently in close proximity to another larger, adult whale and ii) an animal visually estimated to be < 70% of the body length of the adult whale it is accompanying (Sprogis et al., 2017). The 70% cut-off limit was based on empirical measurements of humpback whale mothers and calves within Exmouth Gulf using an unmanned aerial vehicle (Christiansen et al., 2016). Follows were undertaken in good weather conditions (Beaufort sea state ≤ 3), and ceased if there was poor weather (Beaufort sea state > 3), the focal group was lost or the composition of the group became unclear (groups splitting and joining).

During a follow, data were recorded continuously by three researchers through all occurrence sampling (Altmann, 1974). One researcher used a GoPro to record i) the timing of respirations, ii) group splits and joins, and iii) all visible predetermined behavioural events (Table 1). Data from the GoPro were transcribed post-hoc to ensure all events were captured in real-time. A second researcher recorded i) distances from the vessel to the whale(s) using a laser range finder (Bushnell 10 × 42), ii) bearings to the whale(s) from the vessel using a digital compass (Celestron TrekGuide) and iii) swim heading of the whale(s) relative to the research vessel. This information was collected at 1 minute intervals if whales were surfacing frequently, otherwise during each surfacing bout (time period between the first surfacing and the last surfacing before a long dive, de Vos et al., 2013). A third researcher drove the vessel and assisted in keeping track of individual whales with the aid of photo-identification (Canon 50D, 400 mm lens). The research vessel was positioned behind and to the side of the focal group while ensuring minimal changes in speed and gearshifts to

Fig. 1. Areas of operation for swim-with whale tourism vessels in Ningaloo Marine Park (shaded blue area), Western Australia, extending 5 nm (Commonwealth waters) offshore. Vessel launching sites were at Coral Bay, Tantabiddi, Bundegi and Exmouth marina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
minimise disturbance.

In addition to the observations made on the independent research vessel, data were also collected on-board commercial swim-with vessels. Behavioural sampling protocols onboard swim-with vessels followed the same protocols as those recorded from the independent research vessel. Two researchers were present to record data. Whale movement and surfacing pattern data collected from the independent vessel and aboard the swim-with vessels were combined for analyses to increase statistical power.

2.4. Before, during and after scenarios, and vessel approach types

Data during follows were collected before, during and after swim-with interactions. Follows conducted from the independent research vessel were ideally conducted for 30 min in before scenarios (i.e. control), throughout the full duration of the during scenario (i.e. impact), and 30 min after interactions following the departure of the swim-with vessel. During scenarios were defined as when one swim-with vessel was present < 300 m of a focal whale(s). All follows conducted from the swim-with vessels were classified as during.

During a swim-with interaction, the vessel approach type was recorded. Three approach types were defined following Constantine (2001) (Supplementary material 3):

a) In-path: a vessel was driven ahead of the whales' path of travel before turning in front of the approaching whale (> 150 m in ECZ) to intercept the whales' path of travel and place swimmers in the water,

b) Line-abreast: swimmers were placed to one side and ahead of the whales' path of travel within the ECZ, and swimmers would swim over or observe the whales from the side as they swim past,

c) Side approach: a vessel approached the whales slowly and swimmers were placed to one side of the whale and then swam to 30 m from the whale.

To test if the behavioural response of whales differed between vessel approach types, we divided the during scenario into in-path and side/line-abreast approaches. Side and line-abreast approaches were merged into a single approach type due to small sample size and as they are similar in that they give animals the choice to approach swimmers and do not force uninterested animals to interact or change their direction of travel (Constantine, 2001). The response of an animal towards a source of disturbance, such as a swim-with vessel, has also been shown to depend on the initial behavioural state of the animal (Christiansen et al., 2010; Lusseau, 2003). Thus, to account for this, before scenarios were divided into before-travelling and before-resting scenarios. While in-path approaches were generally used to approach travelling whales, side/line-approaches were the most common way to approach resting/stationary whales. Thus, we compared in-path approaches to before-travelling scenarios, and side/line-abreast to before-resting scenarios.

2.5. Data processing: whale positions and interaction zones

Using the GPS position from the research platform (either the research vessel or the swim-with vessel) together with the distance and bearing to the whale, the position (latitude and longitude) of the focal whale(s) was estimated at one-minute intervals or once within a surfacing bout (if greater than 1 min). The location, heading and speed of the swim-with vessel were known from the vessel’s Electronic Monitoring System (EMS), which recorded at one-minute intervals (Department of Parks and Wildlife, 2016). Thus, the distance and heading (towards vessel = 0°, away from vessel = 180°) of the focal whale(s) to the nearest swim-with vessel was calculated post hoc.

Each whale position was further classified into a specific zone, based on the Department of Parks and Wildlife licence conditions (Supplementary material 1). If a swim-with vessel was < 100 m from

<table>
<thead>
<tr>
<th>Behavioural event</th>
<th>Definition</th>
<th>Presumed purpose of behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudopod slap</td>
<td>Whale strikes the surface of the water with the lateral side of the pseudopod and fluke (aka ‘pseudopod throw’, ‘tail breach’).</td>
<td>Potentially several functions, including being agonistic to ward off predators/competitors (Clapham, 2000; Ford and Reeves, 2008).</td>
</tr>
<tr>
<td>Fluke slap</td>
<td>Whale slaps the surface of the water forcefully with the ventral or dorsal side of its fluke (aka ‘lob tail’, ‘tail slap’).</td>
<td>Agonistic to ward off predators/competitors (Pitman et al., 2015), and/or important in mediating social interactions (Kavanagh et al., 2017b).</td>
</tr>
<tr>
<td>Pectoral slap</td>
<td>Whale slaps the surface of the water with its pectoral fin, ventrally or dorsally (aka ‘flippering’ ‘flipper slap’).</td>
<td>Non-verbal communication (Dunlop et al., 2008; Kavanagh et al., 2017b) and/or agonistic towards predators by thrashing their pectoral fins (Ford and Reeves, 2008; Pitman et al., 2015).</td>
</tr>
<tr>
<td>Head slap</td>
<td>Whale strikes the surface of the water with the ventral side of its head, in any direction (aka ‘chin slap’).</td>
<td>Agonistic to ward off predators/competitors (Ford and Reeves, 2008).</td>
</tr>
<tr>
<td>Head lunge</td>
<td>Fast upward thrusting of head forward out of the water at an angle &lt; 40°.</td>
<td>Agonistic to ward off predators/competitors (Baker and Herman, 1984; Pitman et al., 2015; Silber, 1986).</td>
</tr>
<tr>
<td>Breach</td>
<td>Whale leaps head first mostly clear of the water (including full and half breach).</td>
<td>Potentially several functions, including communication (Dunlop et al., 2008; Whitehead, 1985).</td>
</tr>
<tr>
<td>Trumpet blow</td>
<td>Exhales force with, a loud vocalisation (aka ‘whooshing’).</td>
<td>Agonistic to ward off predators/competitors (Ford and Reeves, 2008; Pitman et al., 2015).</td>
</tr>
<tr>
<td>Bubble stream</td>
<td>Underwater stream of bubbles can be seen before the whale surfaces and blows.</td>
<td>Agonistic/threat display mostly seen in competitive pods and are made generally by the principle escort (Baker and Herman, 1984; Clapham et al., 1992).</td>
</tr>
<tr>
<td>Fluke thrash</td>
<td>Whale moves fluke rapidly through the water in a sideways movement (aka ‘fluke swim’, ‘fluke cock’, ‘fluke slash’).</td>
<td>Agonistic towards predators/competitors (Pitman et al., 2015; Tyack and Whitehead, 1983).</td>
</tr>
<tr>
<td>Surfacing</td>
<td>Whale raises head and back out of water without an observed blow (‘no blow rise’).</td>
<td>Passive.</td>
</tr>
<tr>
<td>Surface travel</td>
<td>Whale swims with part of the body breaking the water surface for longer periods than a typical surfacing.</td>
<td>Passive.</td>
</tr>
<tr>
<td>Logging</td>
<td>Whale remains on the surface with no other behaviour visible for &gt; 15 s.</td>
<td>Passive.</td>
</tr>
<tr>
<td>Slip under</td>
<td>Whale submerges, sinking fairly flat in the water.</td>
<td>Passive.</td>
</tr>
<tr>
<td>Round out</td>
<td>Whale submerges exposing the pseudopod but not the fluke (aka ‘peduncle arch dive’).</td>
<td>Passive.</td>
</tr>
<tr>
<td>Fluke dive</td>
<td>Whale performs a fluke-up or fluke-down dive.</td>
<td>Passive.</td>
</tr>
<tr>
<td>Spy hop</td>
<td>Whale raises its head vertically out of the water.</td>
<td>Passive.</td>
</tr>
<tr>
<td>Roll</td>
<td>Whale rolls on its back or side, and pectoral fins can be seen in the air.</td>
<td>Passive.</td>
</tr>
</tbody>
</table>
the whales’ position it was classified as in the ECZ, whereas a swim-with vessel within 100–300 m of the whales’ position was classified as in the ‘approach zone’ (Department of Parks and Wildlife, 2016). All swim-with vessels beyond 300 m of the whales’ position were classified as being outside of the approach zone.

Follows were excluded from analyses if i) before scenarios included whales socialising, to better differentiate between before-travelling and before-resting whales and as the sample size was low, ii) follows included a mixture of in-path and side/line-abreast approaches, to clearly distinguish the effect between these approach types, iii) during follows did not include swim attempts (as during some vessel approaches swimmers were not placed in the water).

2.6. Data analysis – behavioural effects on whales

We investigated the effect of swim-with activities on several behavioural variables including movement patterns (deviation index [DEV] and directness index [DI], heading, swim speed), surfacing patterns (dive duration and respiration rate), and the occurrence of agonistic behaviours. Movement patterns relate to horizontal avoidance strategies where avoidance is associated with changes in direction and increased swim speeds (Williams et al., 2002). Surfacing patterns relate to vertical avoidance strategies where avoidance is associated with increased dive durations and decreased time spent at the surface (Baker and Herman, 1989). Deviation index, directness index and respiration rate were analysed between follows (on a follow level), whilst heading, swim speed, dive duration and the occurrence of agonistic behaviours were analysed within follows (on a data point level). For analyses between follows, the effect of scenario (before-travelling, before-resting, in-path approach, side/line-abreast approach, after) was investigated. For analyses within follows, the effect of scenario and zone (0–100 m, 100–300 m approach zone, 300–10,000 m) was explored. Analyses were conducted in R v3.0.3 (R Development Core Team, 2011).

2.6.1. Movement patterns

2.6.1.1. Deviation and directness index. DEV represents the predictability of a whale’s movement track, and was calculated by taking the mean of the turning angles between consecutive positions within a follow. DEV ranges between 0° (linear movement) and 180° (erratic movement). DI represents the linearity/sinuosity of the track, and was calculated by dividing the net distance (the distance between the first and last position in the track) of the track by the total distance of the track (the sum of the distances of all legs of the track). DI ranges from 0 (circular movement) to 1 (linear movement). The effect of scenario (before-travelling, before-resting, in-path, side/line-abreast, after) on DEV and DI between follows was tested using linear models (LMs). Calf presence was included as a covariate (as calves were swim with, see Section 3.2). To avoid potential bias from tracks with relatively few positions (fewer positions may make a track line straighter), a sensitivity analysis was conducted. Follows with a limited number of positions (< 8) caused a negative bias on the DI \( F_{1,184} = 11.75, P < .001 \). Thus, to remove any bias only follows that had eight or more positions were included in analyses.

2.6.1.2. Heading. The effect of swim-with activities on the heading of humpback whales within follows was investigated using linear mixed effect models (LMMs). The mean heading of the whales in relation to the nearest swim-with vessel was compared among scenarios (before-travelling, before-resting, in-path, side/line-abreast, after) and zones (0–100 m, 100–300 m, 300–10,000 m). Calf presence was included as a covariate. To account for temporal dependence in the data (points within follows were temporally correlated), auto-correlation (the acf function) and partial auto-correlation (the pacf function) plots were produced to visually examine the model residuals for auto-regressive and moving average structures. Based on these plots, a temporal auto-regressive structure with a lag of one within follows was included in the final model. To account for variations in heading between follows, follow ID was added as a random effect.

2.6.1.3. Swim speed. Swim speed (ms\(^{-1}\)) of the focal groups was estimated between every position using the location data (calculated latitude/longitude) of the whales. A speed filter was used to remove positions that showed the whale swimming at unrealistic speeds (> 6 ms\(^{-1}\), threshold based on visual inspection of the frequency distribution of swim speeds). LMMs were used to compare the swim speed of humpback whales among scenarios (before-travelling, before-resting, in-path, side/line-abreast, after). To account for temporal auto-correlation within follows, the model was used with an auto-regressive structure with lag one, and follow ID as a random effect. Calf presence was included as a covariate. The same as for DI, follows with limited number of positions (< 8) caused a negative bias (e.g. overestimation) on the swim speed of whales \( F_{1,182} = 6.41, P = .012 \), which resulted in 94 follows being removed from the analyses to avoid this bias.

2.6.2. Surfacing patterns

2.6.2.1. Dive duration. The surfacing pattern of baleen whales generally consists of a series of shorter dives, during which an animal replenishes its oxygen levels, followed by a longer dive, during which the whale can perform a range of activities (e.g. travelling, singing) (Christiansen et al., 2015). To explore if whales avoided swim-with vessels by spending more time underwater, we investigated the effect of scenario on the long dive duration of whales. To calculate the long dive duration (herein ‘dive duration’), the inter-breathe interval (IBI) of the focal group was calculated from the respiration data (time of every breath). Because individual whales within a group could not always be identified, group IBIs represented the time between any two respirations within a group. Long dives were defined as IBI > 75 s in duration (Kavanagh et al., 2017a). The effect of scenario (before-travelling, before-resting, in-path, side/line-abreast, after) and zone (0–100 m, 100–300 m, 300–10,000 m) on dive duration was tested using LMMs. Temporal auto-correlation was accounted for by adding an auto-regressive structure with a lag of one, and variation between follows was accounted for by adding follow ID as a random effect. The effect of calf presence on dive duration was investigated by including calf presence as a variable.

2.6.2.2. Respiration rate. The respiration rate (number of breaths min\(^{-1}\)) of whales was investigated between follows by dividing the number of breaths by the duration of the follow. To account for variation in group size (i.e. the number of breaths will increase with group size), the number of breaths in a follow was first divided by the number of whales in the group. LMs were used to investigate the effect of scenario (before-travelling, before-resting, in-path, side/line-abreast, after) on respiration rate. Because the respiration rate of baleen whales is likely to increase with swim speed (Christiansen et al., 2014; Williams and Noren, 2009), the average swim speed of the whales during the follow was included as a covariate. The effect of calf presence on respiration rates was investigated, to account for differences in respiration rates between groups with or without calves. Short track durations can lead to an overestimation of respiration rates (Christiansen et al., 2014), thus to avoid this bias we used a loop function to identify the track duration at which this effect became present. This was done by successively removing the tracks with the shortest durations until there was no longer a significant relationship between respiration rate and track duration, and the track duration at which this occurred was then used as the lower threshold value (Christiansen et al., 2014). There was an effect of follow duration on the mean respiration rate of whales \( F_{1,218} = 12.16, P < .001 \), with shorter tracks (< 800 s) being positively biased. This bias was eliminated by removing 59 tracks that were < 800 s in duration (the threshold value identified by the loop function). It is possible that these shorter tracks represented whales displaying avoidance behaviours (e.g.
high swim speeds and consequent respiration rates), which caused the follows to end early (i.e. the whales were lost), however, in good weather conditions whales were not commonly lost, as the research vessel researchers, whale-watch skipper and spotter pilot were all keeping track of the focal group.

2.6.3. Agonistic behaviours

The probability of humpback whales exhibiting agonistic behaviours (Table 1) during swim-with activities was investigated using a binomial generalised linear mixed model (GLMM) with a logit link function. The occurrence of agonistic behaviours was compared among scenarios (before-travelling, before-resting, in-path, side/line-abreast, after) and zones (0-100 m, 100-300 m, 300–10,000 m). Calf presence was included as a covariate in the models. To account for variations between follows, follow ID was used as a random effect in the model. No temporal auto-correlation was detected.

2.6.4. Model validation

Model validation was run to identify potential violations of the assumptions of models. For the LM and LMM models, scatter plots of residuals versus fitted values and residuals against each explanatory variable indicated equal variances (homogeneity) in all models. Normality of residuals was interpreted from residual histograms, which showed no deviation from normality. We also looked for influential points and outliers using leverage and Cook’s distance, but found no extreme values. For the Binomial GLMM, overdispersion was tested by dividing the residual deviance with the residual degrees of freedom, with a ratio value (dispersion parameter, φ) above one indicating overdispersion (the mean of the variance is larger than the mean). No overdispersion was detected.

3. Results

3.1. Research effort and summary statistics

Observations from the independent vessel were conducted on 34 days (n = 300 h), and from commercial swim-with vessels on 49 days (including 54 tours, n = 357 h). Of these tours, 28 were based from Tantabiddi, 19 from Exmouth marina, one from Bundegi, and six from Coral Bay (Fig. 2). The water depth during follows ranged from ~10 m to 140 m, however tour operators generally targeted whales in relatively shallow waters (~20 m) off the back of Ningaloo Reef and ~10 m to 140 m, however tour operators generally targeted whales in

3.2. Behavioural effects on whales

To test if there was an effect of the platform used, it was added as an explanatory variable in the models, however there was no significant effect of platform type in any of the analyses.

3.2.1. Movement patterns

3.2.1.1. Deviation and directness index. Scenario (before, during, after) had a significant effect on the DEV of whales (F4,125 = 4.37, P < .002, R² = 0.123). In before scenarios, resting whales had a higher (t-value = 2.02, P = .046) DEV compared to before-travelling whales (Fig. 3). The DEV was significantly different (t-value = 2.67, P = .009) during in-path approaches compared to before-travelling whales (Fig. 3). There was no significant difference in DEV between side/line-abreast approaches and before-resting whales. The DEV of whales after swim-with activities differed (t-value = 2.40, P = .018) from side/line-abreast approaches, but not from in-path approaches or before behaviours (Fig. 3). There was no effect of calf presence on the DEV of whale groups.

There was a significant effect of scenario (F4,125 = 5.36, P < .001, R² = 0.146) on the DI of humpback whales. The only measured difference in DI was between the after data and before-travelling whales (t-value = 2.09, P = .038) and side/line-abreast approaches (t-value = −2.96, P = .004) (Fig. 4). Calf presence did not affect the DI of humpback whale groups.

3.2.1.2. Heading. The heading of humpback whales relative to the closest swim-with vessel differed between scenarios (F4,187 = 5.62, P < .001). The relative heading was significantly higher (t-value = 3.19, P = .002) during in-path approaches compared to before-travelling scenarios (Fig. 5a). There was no difference in heading relative to the nearest vessel between side/line-abreast approaches (87.7°, SE = 12.04) and before-resting scenarios (Fig. 5a). The relative heading of whales after swim-with activities was significantly lower compared to in-path (t-value = 4.18, P < .001), side/line-abreast approaches (t-value = 2.29, P = .023) and resting scenarios (t-value = 2.54, P = .012) (Fig. 5a).

3.2.1.3. Swim speed. The LMM showed that scenario had a significant effect on swim speed (F4,188 = 8.38, P < .001). In the absence of swim-with vessels, the swim speed of before-travelling whales was significantly faster (t-value = −2.94, P = .004) than for resting whales (Fig. 6). There was a difference (t-value = 2.20, P = .029) in swim speed between in-path approaches and before-travelling whales (Fig. 6). There was no difference in swim speed between side/line-abreast approaches and before-resting (Fig. 6). The average swim speed of humpback whales after swim-with activities was significantly higher than side/line-abreast approaches (t-value = −3.50, P < .001) and before-resting whales (t-value = −2.77, P = .006) (Fig. 6).

3.2.2. Surfacing patterns

3.2.2.1. Dive duration. Scenario (F4,203 = 4.69, P = .001) and calf presence (F3,985 = 16.11, P < .001) had significant effects on the dive duration of whales. Dive duration during in-path approaches was significantly shorter (t-value = −2.08, P = .038) compared to before-travelling whales (Fig. 7). There was no significant difference in dive duration between side/line-abreast approaches and before-resting whales.
whales (Fig. 9). After swim-with activities, the dive duration of whales was longer than for before-travelling (t-value = −2.11, P = .04) and before-resting (t-value = −1.95, P = .05), and significantly longer than during in-path (t-value = −3.75, P < .001) and side/line-abreast approaches (t-value = −2.80, P = .006) (Fig. 7). Irrespective of scenario, the dive duration of groups containing calves was on average 54 s (SE = 13.4) shorter than groups without calves (t-value = −4.01, P < .001) (Fig. 7).

3.2.2.2. Respiration rate. There was no effect of scenario (before, during, after) on the respiration rates of humpback whales. Swim speed also had no effect on respiration rate. Groups containing calves had a significantly (F1,163 = 23.93, P < .001, R2 = 0.128) higher respiration rate compared to groups without calves.

3.2.3. Occurrence of agonistic behaviours

The probability of whales exhibiting agonistic behaviours did not differ between scenarios, however there was a significant difference depending on the distance between the tour vessel and the whales (X2 = 9.11, P = .011). When swim-with vessels were within the ECZ (< 100 m), whales were more likely to perform agonistic behaviours compared to when vessels were in the approach zone (100–300 m) or outside the approach zone (> 300 m) (Fig. 8). Calf presence had no

![Swim-with vessels](image1)

![Independent vessel](image2)

Fig. 2. Research effort tracks (coloured lines represent different days) on-board swim-with vessels (left panel; insert Coral Bay) and the independent vessel (right panel) within the Ningaloo Marine Park, Western Australia.

![Deviation index](image3)

Fig. 3. Humpback whale deviation index during different scenarios; before (travelling and resting), during (in-path and side/line-abreast approaches) and after swim-with activities. Error bars represent 95% confidence intervals. Corresponding letters above bars represent significant differences between scenarios (between follows analysis, n = 130 follows).

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Focal follows</th>
<th>Mean duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>86 (38.4%), composed of travelling = 77 (34.4%), resting = 9 (4.0%)</td>
<td>29.75 min (14.15 SD)</td>
</tr>
<tr>
<td>During</td>
<td>95 (42.4%), composed of in-path = 82 (36.6%), side/line-abreast = 13 (5.8%)</td>
<td>23.28 min (17.22 SD)</td>
</tr>
<tr>
<td>After</td>
<td>43 (19.2%)</td>
<td>23.67 min (17.03 SD)</td>
</tr>
</tbody>
</table>

Table 2

Summary of the behavioural focal follows used in analyses (total = 224).
Influence on the probability of whales performing agonistic behaviours.

3.3. Interactions with calves

Young-of-year calves were present during 19.6% (18 of 92) of follows that included swim attempts. Data from 25 August to 27 October 2018, calculated the number of calves that exceeded 50% of their mother’s length was 36.1% (35 of 97; Fig. 9). Calves could grow to 60% of their mother’s length in this time period, and ranged from 4.3 m to 7.7 m long ($\bar{x} = 5.8 \pm 0.61\ SD$). These empirical length measurements were obtained from an unmanned aerial vehicle as a part of a separate research project (Sprogis et al., unpublished data).

4. Discussion

Humpback whales migrating through the Ningaloo Marine Park were exposed to swim-with activities along their northern and southern migration, from the beginning of August until late October 2016. We evaluated whale behaviour before, during and after swim-with activities.

Findings indicated that during swim-with activities, when vessels were in the whales’ path, whales used horizontal avoidance strategies to avoid the swim-with vessels, by adopting a less predictable path, using higher turning angles to orient away from vessels, and increased swim speeds. Whales also altered their surfacing patterns by decreasing the duration of their long dives towards vessels that were in their path. Documented responses were similar to other studies on the behavioural responses of humpback whales to whale-watch activities (see a list of studies in Supplementary Material 5).

4.1. Behavioural responses of humpback whales towards swim-with activities

During swim-with activities, side/line abreast approaches had no effect on the horizontal movements of the whales. In contrast, during in-path approaches, whales adopted a less predictable path, with greater swim speeds and greater angle of avoidance away from vessels (turning ~90° away). The angle of avoidance was highest when vessels were within 300 m of the whales. Similar responses were documented...
for whale-watching activities on humpback whales off New Caledonia, where > 60% of groups adopted a more erratic swim path, increased the sinuosity of their path within 335 m of the vessel, and increased swim speeds (Schaffar et al., 2013). These findings are also consistent with swim-with activities on southern right whales off Peninsula Valdés, Argentina, where whales showed a less predictable path during swim-with activities (Lundquist et al., 2013). In our study, after swim-with activities, the whales’ heading reduced in angle (compared to in-path and side/line abreast approaches), and paths became more predictable and linear (compared to side/line abreast approaches). These results suggest that the whales travelled away from the swim-with interaction area and/or the whales moving into deeper waters adjacent to the reef, which was visible when inspecting their movement tracks.

 whales increased the duration of their long dives. The increase in dive duration could be due to whales moving away from the swim-with interaction area and/or the whales moving into deeper waters adjacent to the reef, which was visible when inspecting their movement tracks.

4.2. In-path vessel approaches vs. side/line-abreast approaches

During our study, in-path vessel approaches were the most common type (89.8%), predominantly targeting travelling whales (86.6% of in-path approaches). In contrast, of the 10.2% of approaches that used side/line-abreast vessel approaches, 69.2% of these targeted resting whales. During in-path approaches, skippers need to increase vessel speeds to move ahead of travelling whales. The average maximum vessel speed for in-path approaches was 31.5 km h⁻¹ (17 kts), compared to 24.6 km h⁻¹ (13.3 kts) for side/line-abreast approaches. This increase in speed is of concern as with an increase in vessel speed there is an increase in underwater noise (Jensen et al., 2009; Williams et al., 2002). When accounting for the initial behavioural state of the whales (travelling or resting), we found that in-path approaches resulted in a change in the DEV, heading, dive duration and swim speed of whales. In contrast, side/line-abreast approaches did not alter the behaviour of resting whales significantly. This difference in effect size suggests that in-path vessel approaches significantly affected the behaviour of whales along their migration route.

Other studies have also reported that in-path approaches are more invasive and significantly affect the behaviour of cetaceans by causing avoidance responses (Constantine, 2001; Fiori et al., 2019; Machernis et al., 2018; Martinez et al., 2010; Williams et al., 2002). For example, when whale-watch vessels approach in-path of killer whales (Orcinus orca), males evade vessels by swimming in an erratic path (less predictable and more sinuous), and thus travel approximately 17% further than they would in the absence of vessels (Williams et al., 2002). Similarly, when swimmers were placed in-path of bottlenose dolphins (Tursiops truncatus) off New Zealand, dolphins significantly increased their avoidance of vessels over time (Constantine, 2001). Overall, in-path approaches and swimmer placements are not approved in international whale-watch regulations (Carlson, 2013), and are not recommended in the International Whaling Commission (IWC) guidelines (IWC, 1996). Furthermore, under the National Australian Guidelines, it is not permitted to approach whales in-path of their travel (60° no approach zone) within 300 m (Commonwealth of Australia, 2017).
4.3. Swimming with mother and calf pairs

The 2016 swim-with-whale licence conditions stated not to place swimmers in the water with humpback whale calves, however this condition was not strictly followed during the trial partly due to the initial definition of a calf used by the Department of Parks and Wildlife; “a young whale, approximately half the length of or less of adult individuals of its species” (Department of Parks and Wildlife, 2016). This definition did not protect all young-of-year calves from swim-with activities during the swim-with season. Empirical studies in Exmouth Gulf document that calves (< 4 months old) can grow to > 50% of their mothers length (Christiansen et al., 2016). These findings became available to the Department of Parks and Wildlife during the swim-with trial. Subsequently, the Department revised their definition of a ‘calf’ on 23 September 2016 to “a young whale, paler in colour than adults of its species and/or less than 8 metres in length and/or less than two thirds of the length of the adult it is in association with”. From 2017, the definition has been “any humpback whale that is less than two thirds of the length of any adult whale/s which it accompanies”. This updated definition now reflects the actual size of calves in the region (4.3 m to 7.7 m in length).

Overall, groups with calves exhibited significantly shorter dive durations and higher respiration rates compared to other groups, which is expected due to the physiological limits of the calf. Other studies on baleen whales have shown that groups with calves are more sensitive to whale-watch activities, by changing their respiration rate and time spent submerged (Stamation et al., 2010). Off Peninsula Valdés, Argentina, southern right whale calves exposed to swim-with activities show the strongest responses by repeatedly changing their direction of travel and increasing swim speed (Lundquist et al., 2013). While the measured effects of path predictability, heading, dive duration and swim speed was the same for groups with and without calves, the potential energetic consequences of these behavioural changes are likely to be greater for calves and lactating mothers than for other adult whales. During the first months of a calves life they need to grow at a rapid rate so that they can endure the migration to the Antarctic feeding ground (Irvine et al., 2017). To enable this considerable energy transfer from mothers and calves to occur, the calves spend a large proportion of their time (~20%) suckling (Videsen et al., 2017), while the mother rests (Bejder et al., 2019). Over extended periods of time any increase in energy expenditure could become biologically significant for a calf (Cartwright and Sullivan, 2009). Carrying greater energetic costs likely means that mother and calf pairs have the greatest vulnerability to disturbance, which therefore must be limited.

The IWC discourages swimming with calves, and states that calves are “particularly vulnerable to disturbance and require additional protection” (IWC, 2014). Furthermore, under the National Australian Guidelines specifically states that “swimming should not occur with whale or dolphin calves, or pods containing calves” and vessels are not to approach < 300 m of a whale calf (Commonwealth of Australia, 2017). However, in 2017, 2018 and 2019, swim-with licence conditions in the Ningaloo Marine Park were amended to allow swimming with young-of-year calves that were > 50% the length of the mother (representing ~36% of calves). These licence conditions are inconsistent with both national and international best-practice guidelines and recommendations.

4.4. Agonistic behaviours

Humpback whales are one of the most surface-active whale species with a diverse behavioural repertoire (Table 1). These behaviours are used for different functions, including communication within and between groups (Dunlop et al., 2008; Kavanagh et al., 2017b), and agonistic displays for competing for receptive females and towards predators (Clapham et al., 1992; Pack et al., 1998; Pitman et al., 2015; Tyack and Whitehead, 1983). Individual behaviours may serve multiple purposes. For instance, pectoral slapping can function as a non-verbal communication between whales (Dunlop et al., 2008; Kavanagh et al., 2017b) or be an agonistic act towards predators (Ford and Reeves, 2008; Pitman et al., 2015). In our study, the probability of occurrence of presumed agonistic behaviours in whale groups occurred significantly more often when swim-with vessels were < 100 m distance from the whales. Similarly, off Tonga, close approaches of a swim-with vessel increased humpback whale behavioural activity (e.g. pectoral slapping) (Kessler et al., 2013). Likewise for whale-watching activities, humpback whales off Hervey Bay and Sydney performed pectoral slaps (Corkeron, 1995), fluke thrashes and trumpet blows more often when in the presence of vessels (Stamation et al., 2010). Also on a feeding
ground, off Alaska, humpback whales increased their time spent performing surface active behaviours in the presence of whale-watch vessels (Di Clemente et al., 2018).

Globally, swim-with-whale operators reported that whales which were breaching, travelling or in competitive groups were difficult to approach for successful swim-with encounters, whereas singing humpback males proved the most successful individuals for swim-with activities (Gero et al., 2016). Competitive groups are usually associated with fast swimming speeds, erratic movements and high levels of agonistic activity (Baker and Herman, 1984; Tyack and Whitehead, 1983). Any of these agonistic or surface-active behaviours could pose a risk towards human safety if swimmers are close to or in the path of the whales. Although mother-calf pairs are considered by tour operators as ‘ideal’ candidates for swim-with activities, injuries which occurred to human swimmers off WA were from humpback mother and calf groups (Department of Parks and Wildlife, 2017; Sprogis et al., 2017). Specifically, in 2016 two snorkellers were struck with force by the pectoral fin of a mother (one was struck in the ribs and the other received cuts to their hand and ankle) off Ningaloo, and another snorkeller was struck between the legs by the pectoral fin of a mother off the Rowley Shoals, northwest Australia. These incidents highlight the dangers of swimming with large whales.

5. Conclusion

During the 2016 swim-with trial off Ningaloo Marine Park whales displayed horizontal and vertical avoidance responses. Subsequent to the results presented here, the Western Australia Minister for Environment approved the continuation of swim-with-whale activities, which is to transition into a long-term licensed industry by 2021. Most short-term disturbances to cetaceans can be prevented or minimised by adhering to best-practice whale-watching guidelines set by the IWC and the Australian Federal Government (Commonwealth of Australia, 2017; IWC, 1996). Based on best-practice guidelines and the findings from this study, we recommend that some of the current regulations (i.e. in-path approach type and swimming with calves) in the Ningaloo Marine Park are revised.

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Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.151254.

References


Behavioural responses of migrating humpback whales to swim-with interactions in the Ningaloo Marine Park, Western Australia
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Journal of Experimental Marine Biology and Ecology

Supplementary material 1

Fig. 1. Diagram depicting the 2016 swim-with humpback whale licence conditions for commercial swim-with vessels at Ningaloo Marine Park. Approach zone (100-300 m), and Exclusive contact zones (side 50-100 m and in-path 150-300 m) (figure courtesy of Department of Parks and Wildlife 2016).
Table 1
Categories of group activity states, altered from Jenner and Jenner (2011).

<table>
<thead>
<tr>
<th>Activity state</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Socialising</td>
<td>Whales observed physically interacting with each other – often with body contact, and/or exhibiting surface-active behaviours.</td>
</tr>
<tr>
<td>Resting</td>
<td>Whales laying stationary submerged or at the surface, not swimming and exhibiting surface behaviours.</td>
</tr>
<tr>
<td>Travelling</td>
<td>Whales exhibiting persistent directional movement, with low levels of surface-active behaviours.</td>
</tr>
<tr>
<td>Milling</td>
<td>Whales with no real pattern or direction of movement, e.g. whales showing frequent changes in swim direction (&gt;20° deviation approx.) within three surfacing bouts or towards an obstacle that would prevent further migration travel (i.e. the reef).</td>
</tr>
</tbody>
</table>
**Supplementary material 3**

**Fig. 1.** Whale-watch vessel approach types for swimmer placement, where swimmers (black dots) entered the water from the rear of the vessel. A) In-path: a whale-watch vessel was driven ahead of the whales’ path of travel before turning in front of the approaching whale (>150 m in ECZ A) to intercept the whales path of travel and place their swimmers in the water, aka ‘J-approach’ and ‘leap-frogging’ (Constantine, 2001; Constantine and Baker, 1997; Williams et al., 2002); B) Line-abreast: swimmers were placed to one side and ahead of the whales’ path of travel within the ECZ, and swimmers could swim over or observe the whales from the side as the whales swum past (Constantine, 2001; Constantine and Baker, 1997); and C) Side approach: vessel approached slowly and swimmers were placed to one side of the whales where swimmers swam to 30 m of the whale.
Supplementary material 4

Table 1
A breakdown of the data collected during follows in before, during or after situation.

<table>
<thead>
<tr>
<th>Situation</th>
<th>Whale positions</th>
<th>Whale respirations</th>
<th>Surface active behavioural events</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>1,370 (45.6%)</td>
<td>4,916 (43.6%)</td>
<td>2,286 (47.9%)</td>
</tr>
<tr>
<td>During</td>
<td>1,152 (38.4%)</td>
<td>4,287 (38.1%)</td>
<td>1,630 (34.2%)</td>
</tr>
<tr>
<td>After</td>
<td>480 (16.0%)</td>
<td>2,063 (18.3%)</td>
<td>855 (17.9%)</td>
</tr>
<tr>
<td>Total</td>
<td>3,002</td>
<td>11,266</td>
<td>4,771</td>
</tr>
</tbody>
</table>
**Supplementary material 5**

Table 1

Peer-reviewed scientific papers on the behavioural effects on humpback whales from whale-watching and swim-with tourism (*). Papers listed from 1995 onwards in chronological order. Behavioural effects: “−” = not studied, “↑” = Increased, “↓” = decrease. Note that swim-with activities should not be directly compared with whale-watching activities, as the approach types and distances vary, however in this table whale-watching activities have been included due to the lack of swim-with studies conducted on humpback whales.

<table>
<thead>
<tr>
<th>Author and Location</th>
<th>Location type</th>
<th>Effects on calves</th>
<th>DEV, DI, Heading</th>
<th>Swim speed</th>
<th>Dive duration</th>
<th>Respiration rate</th>
<th>Surface behavioural events</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Corkeron, 1995). Hervey Bay, Australia.</td>
<td>Resting/nursing ground.</td>
<td>Pods with calves more likely to dive, and exhibit surface active behaviours when vessel &lt;300 m.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>No effect.</td>
<td>↑ dives compared to slip under. Breaches and pec slaps common in presence of vessel.</td>
<td>Fluke slaps and peduncle slaps occurred in groups without calves in the presence of vessels.</td>
</tr>
<tr>
<td>(Scheidat et al., 2004). Machalilla National Park, Ecuador.</td>
<td>Breeding ground.</td>
<td>–</td>
<td>No effect.</td>
<td>↑</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Agonistic behaviours observed towards vessels.</td>
</tr>
<tr>
<td>Study</td>
<td>Location</td>
<td>Activity</td>
<td>Effect on Calf Survival</td>
<td>Fluke</td>
<td>Dive Durations</td>
<td>Behavioural Changes</td>
<td>Avoidance</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>(Weinrich and Corbelli, 2009). Southern New England, USA.</td>
<td>Feeding ground.</td>
<td>No effect on long-term calving rate or calf survival.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>(Stamation et al., 2010). South-east coast, Australia.</td>
<td>Migration route.</td>
<td>Calf groups were more sensitive to interactions.</td>
<td>–</td>
<td>↑</td>
<td>↑(groups with calves).</td>
<td>–</td>
<td>–</td>
<td>17% of pods showed signs of avoidance.</td>
</tr>
<tr>
<td>(Gulessarian et al., 2011). Sydney, Australia.</td>
<td>Migration route.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>↓deep, long dives durations. ↑short, shallow dive duration.</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>(Schaffar et al., 2013). Cap Ndoua, New Caledonia.</td>
<td>Breeding ground.</td>
<td>–</td>
<td>↑DEV and ↓DI.</td>
<td>↑</td>
<td>↑</td>
<td>–</td>
<td>–</td>
<td>Over 80% significantly changed their behaviour.</td>
</tr>
<tr>
<td>(Kessler and Harcourt, 2013)*. Ha'apai Island group, Kingdom of Tonga.</td>
<td>Breeding ground.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>↑whale activity (e.g. pec slap, breach).</td>
<td>Whales responded quickly to swimmers loud/splashing than to quiet approaches.</td>
<td>–</td>
</tr>
<tr>
<td>Study (Ref)</td>
<td>Location</td>
<td>Behaviour (Changes)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>(Avila et al., 2015). Bahía Málaga, Columbia.</td>
<td>Breeding ground.</td>
<td>–</td>
<td>–</td>
<td>↑</td>
<td>number of dives/min.</td>
<td>–</td>
<td>↑breaching.</td>
<td>← in resting.</td>
</tr>
<tr>
<td>(Di Clemente et al., 2018). Juneau, USA.</td>
<td>Feeding ground.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>←</td>
<td>←</td>
<td>←</td>
<td>↑</td>
</tr>
<tr>
<td>(Garcia-Cegarra et al., 2019). Los Organos, Peru.</td>
<td>Breeding ground.</td>
<td>↓Swim speed, ↑dive duration, ↓respiration rate in groups with calves</td>
<td>↓DI during, ↑DI after.</td>
<td>↑</td>
<td>↓</td>
<td>↑</td>
<td>←</td>
<td>←</td>
</tr>
<tr>
<td>(Fiori et al., 2019)*. Vava’u, Kingdom of Tonga.</td>
<td>Breeding ground.</td>
<td>Study focused on mother/calves.</td>
<td>↑reorientati on rate (groups with calves).</td>
<td>–</td>
<td>↑(groups with calves).</td>
<td>↓(although not significant).</td>
<td>←</td>
<td>–</td>
</tr>
<tr>
<td>This study*. Ningaloo Marine Park, Australia.</td>
<td>Migration route.</td>
<td>↓Dive duration, ↑respiration rate in groups with calves.</td>
<td>↑DEV and heading during in-path approaches.</td>
<td>↑during in-path approaches.</td>
<td>↓long-dive duration during in-path approaches.</td>
<td>No effect for groups without calves.</td>
<td>↑agonistic behaviours (&lt;100 m).</td>
<td>Most common approach type was in-path (89.8%).</td>
</tr>
</tbody>
</table>
References


