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Effects of dolphin-swim activities on the behaviour of an Indo-Pacific bottlenose dolphin population off the south coast of Mozambique

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ABSTRACT

Swim-with-dolphin (SWD) activities are popular but can negatively impact target populations. It is important to consider the behavioural responses of dolphins, and quantify the impact on individuals and populations, as well as maximise opportunities for sustainable tourism that benefits socio-economic growth while encouraging pro-environmental behaviour. This is of relevance in `developing countries, where ecological studies are scarce and tourism industries may have developed before science-based management measures were implemented.

This study aimed to determine the effects of SWD tourism on the behaviour of resident Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Ponta do Ouro Partial Marine Reserve (PPMR), Mozambique. Markov-chain models were used to describe dolphin behaviour transition probabilities in different tourism contexts between 2007 and 2009 (low tourism) and 2017–2019 (high tourism). Results detected significant short-term changes in the behaviours of dolphins. In the early years (2007–2009), dolphins were likely to remain in their preceding behaviour if they were resting, travelling, and foraging. However, for later years (2017–2019) this only occurred if they were travelling. Overall, after tourist swims, and under both tourism contexts, dolphins were more likely to travel and less likely to socialise, rest, or forage. The findings raise concerns that, despite current management measures, SWD activities still affect dolphin behaviour and impose short-term negative effects to their activity budget. Our study recommends time- and area-closures, speed restrictions, and mandatory training programmes to all SWD staff. Given that SWD and whale-watching activities take place along the coast of Mozambique, national regulations are urgently needed to minimise potential long-term negative effects on cetacean populations.

1. Introduction

Cetacean tourism, particularly "swim with dolphin" (SWD) activities, is globally increasing in popularity (Hoyt, 2018). This type of tourism can support local economies, especially in developing countries (Cisneros-Montemayor et al., 2010; Pérez-Jorge et al., 2017b). The activity also has the potential to enhance knowledge and conservation awareness to local communities and tourists partaking in the activities (Cecchetti et al., 2018; Jacobs and Harms, 2014). However, tourism can have negative impacts on the target cetacean populations (Fumagalli et al., 2018; Pirotta et al., 2018; Shawky et al., 2020).

Dolphins can react to tourism vessels through various behavioural changes, such as changes in activity, speed, direction of movement, diving behaviour, group formation, and vocalisations (Bejder et al., 1999; Heiler et al., 2016; Lusseau, 2003; Martinez et al., 2011; Meissner et al., 2015; Pérez-Jorge et al., 2016; Pirotta et al., 2015, 2018; Williams et al., 2006). Studies focused on an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population in southern Kenya reported that tourism affected individuals' activity budgets with a decrease in time spent travelling and resting, while diving periods increased, possibly signifying increased avoidance to boats and swimmers (Pérez-Jorge et al., 2017a, 2017b). Similar results were presented by Christiansen et al. (2010) for the same species in Zanzibar, Tanzania. These negative impacts are particularly disturbing where individuals are resident or show high site-fidelity, due to the cumulative effect of daily disturbance (Cecchetti et al., 2018). Other long-term impacts have been reported

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including area avoidance, reductions in female reproductive success and declines of relative abundance (Bejder et al., 2006; Christiansen et al., 2010; Pérez-Jorge et al., 2017a, 2017b).

Many SWD activities take place without an in-water guide or have a high number of swimmers, which can lead to bad conduct (e.g. flash photography, touching the dolphins). The SWD industry is still relatively new and under-studied, with limited information available on the swimmers' short and long-term effects on dolphins. It is important to understand the effect of SWD activities on dolphins, in order to effectively regulate tourism activities minimizing anthropogenic disturbance. This is especially important in developing countries where legislation for whale-watching and SWD activities is still relatively young, and, in many cases, the industry grows unregulated and the impacts unrecorded. Numerous studies report that SWD activities have the potential to invoke stronger behavioural responses, the boat's proximity to the animals to ensure a successful dolphin-swimmer encounter (Lundquist et al., 2013), has been found to increase stress for the animals (Bas et al., 2017; Steckenreuter et al., 2012b). Studies on spinner dolphins (*Stenella longirostris*) in Hawaii and Egypt, where swimming with wild dolphins is popular, have detected a decline in abundance potentially caused by increased SWD pressure in dolphin resting areas (Fumagalli et al., 2018; Tyne et al., 2016).

The present study took place over a 12-year period (2007–2019) in the Ponta do Ouro Partial Marine Reserve (PPMR) in Mozambique.

This Marine protected area (MPA) uses zoning to manage the activities of different groups. There are two distinct management zones, a Restricted Zone and a Multiple use Zone. In the latter, several activities such as scuba-diving, SWD, swimming and recreational fishing is allowed (DNAC, 2009).

Ponta do Ouro bay is the main destination in the country for SWD activities (DNAC, 2009). SWD activities have been taking place in this bay since 1994. Up to 2010, no regulation existed to guide these activities and, it was with this in mind that in 1996 the first operator, Dolphin Encountours Research Center (DERC), with the assistance of researchers from South Africa, prepared a voluntary CoC (Table 1). This code was later revised and adopted by the management of the reserve (DNAC, 2009). A peak season CoC was voluntarily adopted by all cetacean operators in 2017 (Fig. 1). This stricter version of the code reduces the amount of swim attempts, groups of dolphins approached, and minutes spent with the animals (Table 1 in bold).

Table 1
Code of conduct developed by authors and DERC members (AG and DR) and adopted by the PPMR. In bold are voluntary restrictions adopted during peak season, exclusively.

Boat code	Swim code
No unauthorized vessels to approach within 300mts	Remove only litter
Approach from the side and leave seaward gap	Don't touch nor collect shells and corals
No chase, herd, catch, kill, harass, feed or disturb	No swimming with newborns
No trawling if dolphins are present, keep reel in	No diving down, remain on the surface
Keep slow steady speed (<5 km), avoid sudden changes when bow-riding	Don't swim after or towards dolphins, wait for their approach
No approach with Jet skis	No underwater scooters
Animals have right of way	No underwater flash photography
Avoid mother/calf pairs	Only enter water with authorized personnel
Keep noise to minimum, avoid shouting, whistling etc	Don't touch the dolphins, keep arms close to your body
Do not pursue if they move off	Avoid abrupt movements and loud noises
One vessel within approach zone (300mt)	Maximum swim time of 20 min
Maximum disturbance time of 20 min	**Only one swim attempt**
Only one dolphin group approached per trip	

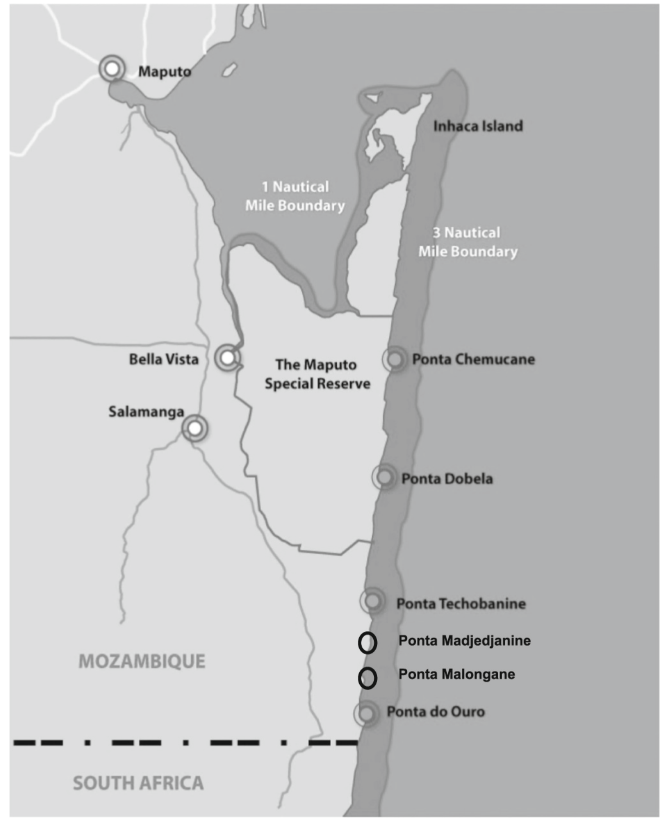

Fig. 1. Map of the PPMR. It also indicates some of the bays in the reserve. This study covered the first three bays (Ponta do Ouro, Ponta Malongane and Ponta Madjedjanine).

The resident population of Indo-Pacific bottlenose dolphins in the PPMR is the main focus of the SWD industry in Mozambique (Rocha et al., 2020). The population has an estimated 300–350 individuals identified using photo-id techniques (pers.comm, Rocha).

Monitoring of behavioural changes has been widely used to determine the effect of boat and swimmers' on the cetaceans. Many studies have created Markov chains and used behavioural budgets as a tool, to asses this disturbance (Cecchetti et al., 2018; Christiansen et al., 2010; Fumagalli et al., 2018; Meissner et al., 2015; Pérez-Jorge et al., 2017a; Shawky et al., 2020). The measurement of behavioural budgets can be used to make comparisons among the same species in different habitats, for the same population at different times and among different individuals or social structures (Steiner, 2011).

The aim of the current study is to investigate how SWD tours affect the behavioural state of the PPMR dolphin population and investigate how these changes alter behavioural budgets over different time frames. First, we assessed seasonal boat traffic to quantify vessel abundance and behaviour. Second, we used Markov chain analysis to estimate the probability of dolphins changing between different behaviour states (e.g., travelling, socialising, milling, resting, and foraging) prior, during and at the departure of tourism boats. Finally, we investigated whether behavioural changes altered the dolphins' overall behavioural budgets. Findings from this work will provide original data from this region, allow for informed decision-making by PPMR managers, as well as offer guidance to operators who aim to improve the quality and sustainability of their tourism activities.

2. Material & methods

2.1. Study site

The PPMR stretches for 86 km along the coast from the border with South Africa to its northernmost point past Inhaca Island. The reserve protects 678 km^2 of marine space, of which 6 % is a no-take zone (Daly et al., 2015). The area has mild winters and warm tropical summers, with tourists all year round; however, there are still distinctive peak seasons during the Christmas and Easter holidays. Tourism operators have anecdotally observed that during these peak seasons the quality of the swimmer-dolphin interactions decreased, with dolphins avoiding, not interacting, or spending less time around the boats and swimmers.

Ponta do Ouro is a small village, located inside the PPMR (Fig. 1), known for its year-round marine activities including diving, fishing, whale watching, and dolphin swimming. Marine operations are mostly owned and managed by South Africans (Lucrezi et al., 2017; Lucrezi and Saayman, 2017) and tourists are also mostly South African, from a wide range of age groups (Lucrezi et al., 2017; Rocha et al., 2020).

The area suffers from anthropogenic pressures, such as unregulated and exponential coastal development, littering, and overfishing (Lucrezi and Saayman, 2017), as well as an increased amount of private and commercial tourism vessel traffic (pers.comm Goncalves 2018).

SWD activities occur on a daily basis by the four permitted operators that take customers on semi-rigid inflatable boats. The operators are distributed in three bays, with the two most frequent ones (conducting at least one daily trip) based in Ponta do Ouro. A third operator has a permanent base in Malongane's Bay dive centre but caters for a smaller village and therefore conducts less trips. The fourth operator is incorporated in a small capacity five-star resort and caters only for the resort's clients, also resulting in very few trips.

2.2. Data collection

Non-systematic boat-based surveys were conducted from Dolphin Encountours Research Center's (DERC) boat during dolphin swim/observation trips. The operator used a semi-rigid inflatable boat with capacity for 16 people (including crew) and two four stroke, 90HP, Suzuki engines. The survey was opportunistic and observation effort varied as it was limited to favourable environmental conditions and minimum economic requirements (minimum of four paying customers). An observer was positioned, standing, next to the skipper and looking ahead (180° angle of search). A second observer was positioned standing at the back of the boat increasing area coverage. No further equipment was used when searching for dolphins given that environmental conditions hardly ever allow for the safe use of binoculars or cameras. Photographic data collection only took place when the boat found a group and decreased its travelling speed.

DERC launched from the Ponta do Ouro launch site, then followed a standard protocol of driving along the coast, approximately 500 m behind backline (i.e. where the waves break). Initially heading south towards the border with South Africa (1.5 km from the launch site), if no dolphins were encountered the boat would then proceed north for a maximum length of 15 km. The duration of the trip typically lasted 1–1.5 h.

When dolphins were sighted, data was collected, by the first observer, using a group follow protocol (Mann, 1999), with the primary behavioural state based on the activity of >50 % of the group members (Shawky et al., 2020; Stockin et al., 2008). A group was defined as individuals engaging in similar behaviours with close-group cohesions (<50 m) (Bas et al., 2017). Behaviour definitions are presented in Table 2 (Shane et al., 1986).

Duration of the group follow was limited by the PPMR regulations; due to the maximum disturbance time of 20 min per group, operators are only allowed to approach one group per trip in peak season, and if the dolphins display avoidance behaviours the boat must leave. Therefore, during low season researchers could collect data and proceed to find another group, but during peak season would observe only one group per trip for the maximum time of 20 min. These limitations were voluntarily adopted in 2015, by the operators, after a decline in swim-quality was observed during peak seasons. Consequently, during the earlier period of this study, there was no time constraint and observers could remain with the dolphins for an unlimited time.

Table 2
Definitions of behavioural states used in this study (adapted from Cecchetti et al., 2018; Constantine, 2001; Filby et al., 2017b; Lusseau, 2003; Steckenreuter et al., 2012b).

Behavioural state	Definition
Foraging (F)	Dolphin involved in any effort to pursue, capture and/or consume prey, as defined by observations of fish chasing (herding), coordinated deep and/or long-diving and rapid circle swimming. Prey can often be observed at the surface. Many non-coordinated re-entry leaps, fast changes in direction and long dives.
Milling (M)	Non-directional movement, frequent changes in bearing which prevent animals from heading in a specific direction. Different individuals can head in different directions at the same time within a group, but they keep together.
Resting (R)	Tight group cohesion, less than one body length apart. Slow maneuvers with little evidence of forward propulsion. Slow and often synchronous surfacing.
Socialising (S)	Diverse interactive events among group members (social rub, aggressiveness, chasing, mating and other physical contact). Aerial behaviours such as breaching.
Travelling (T)	Noticeable headway on a persistent direction and constant speed. Usually faster than the idle speed of boat. Group has constant and short dive intervals.

During follows, data were collected three times, T0 = Approach (at arrival of boat), T1 = In-water (in-water dolphin-human interaction), and T2 = Leave (after swim-with activities), similar to methods applied by Sprogis et al. (2020). Distance at first sight can vary between 500 and 200 m. Although it is worth noting that the dolphins will likely be aware of the vessel beyond these distances (especially the vessel noise). Regardless, this was considered the "Approach" period in the present study.

Swimming with the dolphins was dependent on the group's behavioural state, location and environmental conditions, for safety of both humans and dolphins. If there was no swim-with attempt, only T0 and T2 were collected, and the follow was not included in the present analysis.

DERC used the "line abreast" (parallel approach) for observation and once the swimmers were ready to get in the water the approach would change to "in path" (J approach; Sprogis et al., 2020). In this case, the boat would drive 100 to 150 m ahead of the dolphin group and drop the clients in their path, giving the swimmers time to acclimatize and the dolphins time to decide whether they wished to avoid or engage with the humans.

The group follows ended when the dolphin group disappeared or presented an avoiding behaviour (e.g. tail slapping on the surface, charge without physical contact, jaw clapping towards swimmers), when weather conditions deteriorated, or when the 20 min observation time was reached.

2.3. Vessel data collection

Soon after the PPMR was established, a data collection protocol was implemented to monitor vessel traffic. The number of vessels, type of vessels (i.e., boat, jet ski, kayak), number of people, and the activity for each vessel were recorded by park rangers based at the Ponta do Ouro launch site. These rangers remain at the site from 7:30 am until the last vessels leave the water each day, and record data whenever a new vessel arrives. No vessels are allowed once the sun sets. The PPMR has provided access to all vessel data collected for the years of 2010 to 2020. For the purpose of this study, only the years between 2011 and 2019 will be included, on account of inconsistent data collection for 2010 (trial year) and beach closure due to COVID19 from March 2020 to April 2021.

Since the reserve was only implemented in 2009, no previous vessel data are available. However, dolphin-swim vessel (DSV) numbers for the early years of 2007 to 2009 can be obtained from DERC, given that it was the only dolphin boat operating in the area at that time. Descriptive statistics were used to investigate the distribution of vessels across years and activities.

The vessels were organized in three broad categories:

1. Diving: recreational diving with licensed diving operators, no private boats allowed to dive.
2. Snorkelling: SWD and Ocean Safari (OS) activities were merged despite being advertised separately and OS not being licensed for cetacean tourism. However, both activities, which are currently offered by different operators, cover the same areas in search of wildlife to observe/swim with, and tourists misguidedly choose OS to SWD under the impression that both activities can engage with cetaceans. OS are a novelty and yet to be regulated by the PPMR's management plan, leaving space for interpretation.
3. Fishing (Boats and Jet skis): Recreational fishing can be carried out from private boats or jet skis, as well as from licensed recreational fishing operators; no commercial fishing is allowed within the PPMR boundaries.

Private boats used for leisure trips are minimal and therefore excluded. Jet skis are only allowed for recreational fishing and thus are included in the fishing category.

2.4. Data processing

2.4.1. Transition probabilities

To determine the effects of SWD activities and the effect of tourist boats on the dolphin population, we used first-order Markov chain modelling, which estimates the transition probabilities between the preceding and succeeding behavioural states, on the assumption that no activity alters the probability of an activity occurring after the immediately subsequent activity (Lusseau, 2003; Shawky et al., 2020). There are two different timeframes to analyse. First we compared dolphin's behaviour at T0, T1 and T2. We further compared dolphin's behaviour under different anthropogenic pressure. For instance, when there was still only one operator in the area (Early = 2007–2009) to when tourism increases led to four operators in the area (Late = 2017–2019). Similar methods were used by other investigations (Christiansen et al., 2010; Filby et al., 2017a; Meissner et al., 2014; Shawky et al., 2020). This way, comparisons could be made not only between the preceding behaviour (when the boat approaches) and succeeding behaviour (when swimmers leave) (Sprogis et al., 2020), but also between years where tourism was low and when it increased (Toro et al., 2021).

Four contingency tables were created for the number of times a succeeding behaviour was observed following a particular preceding behaviour, two for Early years (T0 > T1; T1 > T2) and two for Late years (T0 > T1; T1 > T2). The four contexts will from now on be referred to as: E1 (Early years, Approach to In-water), E2 (Early years, In-water to Departure), L1 (Late years, Approach to In-water), and L2 (Late years, In-water to Departure).

Z-tests were conducted to determine the statistical significance of individual transitions probabilities (Bas et al., 2017; Shawky et al., 2020; Stockin et al., 2008) between the four contingency tables (E1, E2, L1, and L2). All Z-Tests were conducted using an online calculator from EpiTools (https://epitools.ausvet.com.au/ztesttwo).

2.4.2. Behavioural budgets

The behavioural budgets (i.e. overall proportion of time dolphins spent in each behavioural state) were calculated based on transition probabilities. These were arranged in matrices (one for each context), which were used to calculate the left eigenvectors of the dominant eigenvalues of each matrix (Matlab Version 2014a, based on code provided in Caswell, 2001). This produced five left eigenvectors for each of the four vessel conditions, representing each of the five activity states. To translate these into behavioural budget percentages, the proportion that each left eigenvector contributed to the sum was calculated. These were then assessed via *Z*-test for proportions to compare all contexts (Lusseau, 2003).

3. Results

3.1. Vessel and SWD activities numbers

Between 2011 and 2019, 39,206 boats and 4312 Jet Skis were recorded in the PPMR, 5241 of which are operating SWD activities.

When assessing the total number of vessels per year between 2011 and 2019 (Fig. 2) some fluctuation is observed with a slight overall increase. A traffic increase is primarily observed for Diving (22 %; n = 567) and Dolphin and Ocean Safari trips (20 %; n = 157). Fishing activities indicate a decrease (28 %; n = 424).

The mean number of SWD trips per year (Fig. 3) increased 38 % between 2007 and 2019. If the OS trips are included, this increase rises to 51 %. Fig. 4 presents a monthly breakdown of SWD activities where tourism peak seasons such as Easter holidays (March and April) and Christmas/New Year/end of academic year holidays (December), are clearly identifiable by an estimated traffic increase of 50 %. When comparing early and late years an estimated increase of 40 % is observed. The slight increase in the months of July and August coincides with European summer holidays and the humpback whale (*Megaptera novaeangliae*) migratory season.

3.2. Survey effort

Data were collected during commercial SWD activities from 2007 to 2009 (early years) and 2017 to 2019 (late years). A total of 1168 launches, and 597 h were spent for the early years condition, and 785 launches and 312 h spent following during late years conditions, resulting in 870 behavioural transitions including for E1, 992 for E2, 645 for L1 and, 649 for L2.

3.3. Behavioural transitions

The temporal dependence between behaviours was significantly affected by swimmer's presence in both early and late years.

For all of the four contexts, transition probabilities indicated that dolphins were most likely to continue resting if that was the preceding behaviour (Fig. 5). For both E1 and L1, socialising was most likely to remain (Fig. 5a and c). Likewise, dolphins were most likely to transition from travelling to socialising, foraging to socialising, and milling to socialising under the same context. Furthermore, under the E2 and L2 contexts (Fig. 5b and d), dolphins were most likely to transition from foraging to travelling, and socialising to travelling.

Similarly, during L2, dolphins were most likely to continue travelling or resting if those were their previous states, and transition into travelling from socialising and foraging (Fig. 5d).

Some behaviours and impact contexts presented small sample sizes and therefore were not statistically tested. Out of the 100 possible combinations of behaviour transitions under the four contexts (E1, E2, L1, and L2), a total of 50 statistical comparisons were possible, of which 26 behavioural transitions showed statistically significant differences ($\alpha = 0.05$). Due to the amount of significant *Z*-test results, these are presented in Table 3 with an indication of probability of increase or decrease. There were four statistically significant transitions when comparing the impact of swimmers entering the water between E1 and L1, these were an increase in resting-resting, decrease in resting-

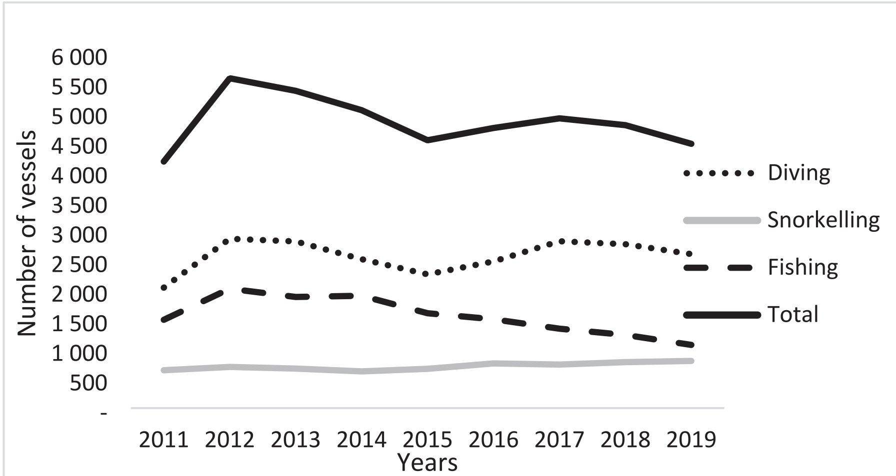

Fig. 2. Variation of total vessels per activity type from 2011 to 2019. All activities relate to tourism, Diving: recreational diving with operators, Snorkelling: Swim-with-dolphin and Ocean Safari trips, Fishing: boat and Jet Ski recreational fishing and, Total: full number of vessels for all recreational activities.

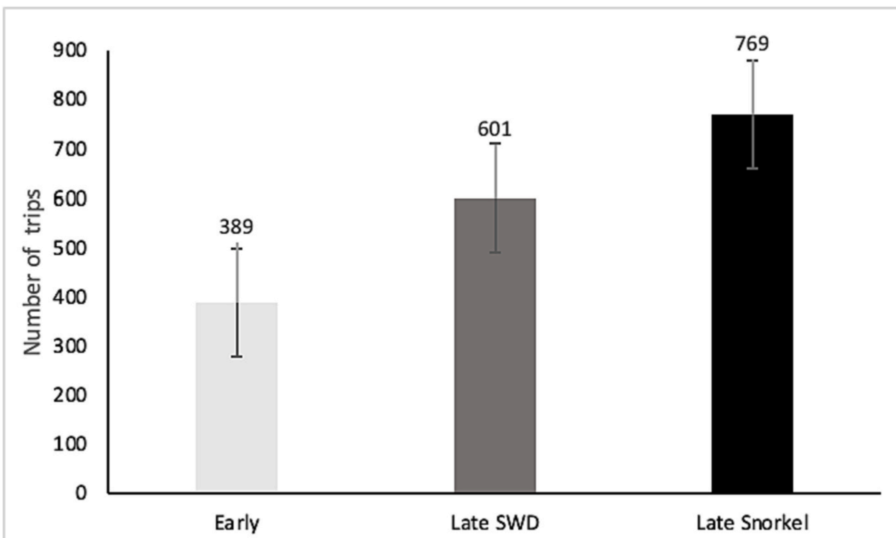

Fig. 3. Mean number of trips per year for SWD in early (2007–2009) and late years (2017–2019). And, mean number of trips per year for Snorkelling in late years (2017–2019).

socialising, decrease in socialising-resting and increase in socialising-socialising. When comparing the dolphin's behaviour at boat departure (E2 and L2), seven transitions were significant namely: increase of travelling-travelling, resting-resting and socialising-travelling, and a decrease of travelling-resting, resting-travelling, socialising-resting, and socialising-socialising. The comparison between E1 and E2 resulted in the greatest number of significant transitions, totalling 10. Specifically, the increase of travelling-travelling, resting-travelling, milling-travelling, foraging-travelling, foraging-foraging, and socialising-travelling; and the decrease of travelling-socialising, resting-socialising, milling-socialising, and socialising-socialising. Finally, five transitions were obtained for the late years (L1 and L2) with increase for travelling-travelling, foraging-travelling, and socialising-travelling, and decrease for travelling-resting and socialising-socialising.

Overall, the probability of most behaviours transitioning to travelling increased and to socialising decreased. When considering the increase of traffic and tourism over the years (Early-Late) the probability of dolphins remaining resting (i.e. not transitioning) increased.

3.4. *Behavioural budgets*

When analysing the early years (2007–2009) behavioural budget comparisons indicated that dolphins spent a greater proportion of time travelling ($z = 9$, $p < 0.001$) and less time socialising ($z = 12.1$, $p < 0.001$) after the departure of swimmers then prior to their approach. When the later years were analysed (2017–2019) the proportion of time spent travelling was also significantly increased ($z = 8.3$, $p < 0.001$), as well as time spent foraging ($z = 2.1$, $p = 0.036$), whereas resting decreased ($z = 3.0$, $p = 0.003$) and so did socialising ($z = 8.5$, $p < 0.001$), after the departure of swimmers then prior to their approach. The proportion of time spent in the different activity states was not significantly different between early and late years (all $p > 0.05$) (Fig. 6).

4. Discussion

The aim of the current study is to investigate how SWD tours effect the behavioural state of the PPMR dolphin population and investigate how these changes alter the behavioural budgets over two different time

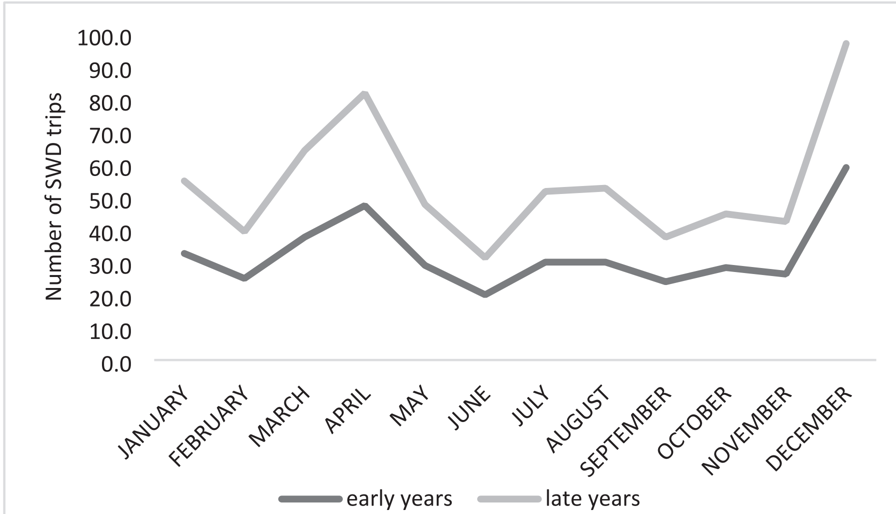

Fig. 4. Mean number of SWD trips per month for the early (2007/08/09) and late (2017/18/19) years.

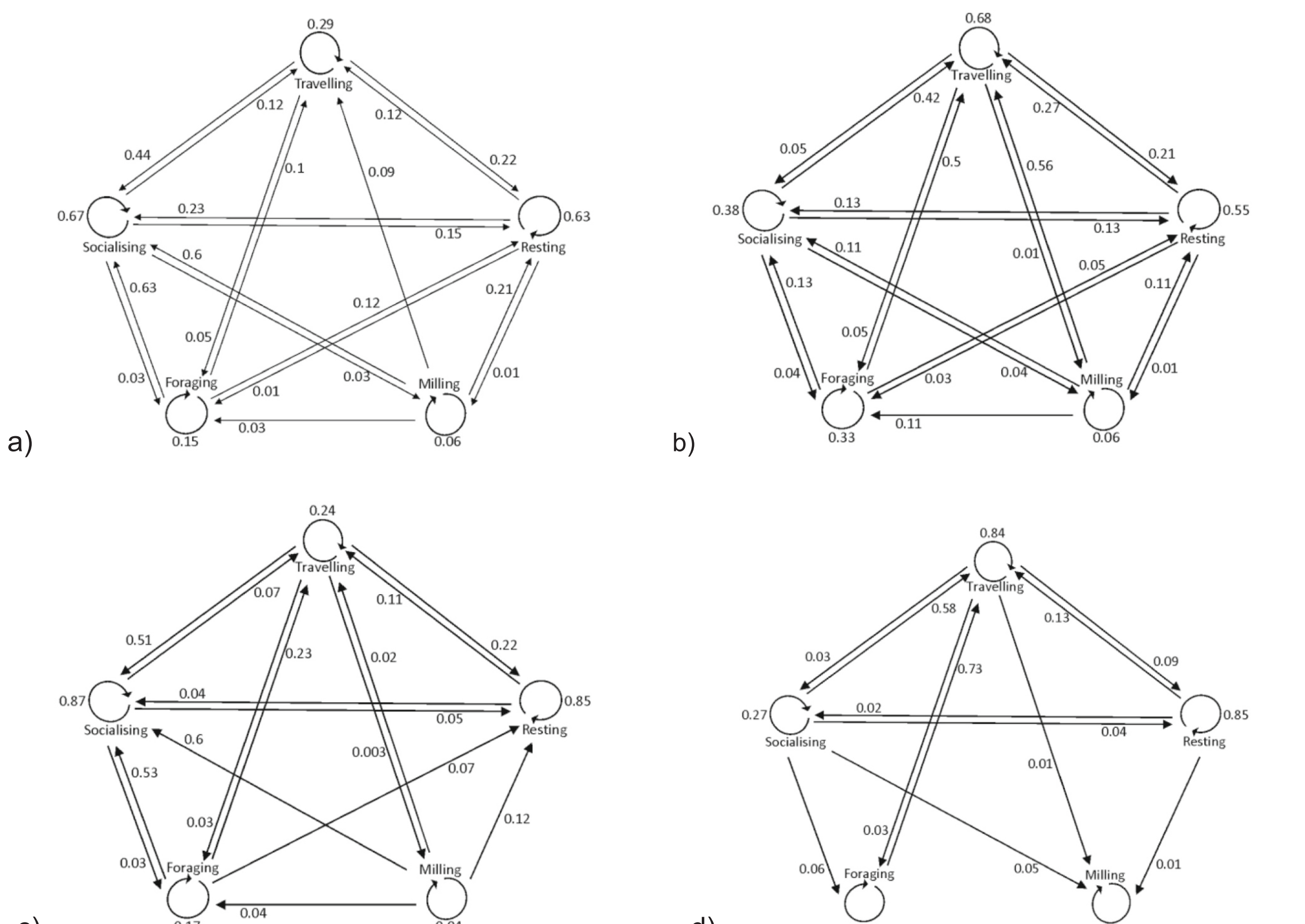

Fig. 5. Markov chains representing probabilities in behavioural state transitions: a) E1, boat approach to swimmers in water; b) E2, swimmers in water to boat departure; c) L1, boat approach to swimmers in water; d) L2, swimmers in water to boat departure. For definitions of each activity state see Table 1.

frames. Significant short- and long-term changes in the behaviours of dolphins were detected as a consequence of SWD interactions.

While assessing the distribution of vessels across years, results showed an overall increase of traffic and that dolphin groups were approached by SWD vessels almost twice as much during peak season in comparison with other times. Similar findings were reported on an Indo-Pacific bottlenose dolphin population off Port Stephens, Australia, where groups were approached 3 times per day in winter and 6 times per day in summer (Steckenreuter et al., 2012a, 2012b). The repeated disruption of resting, foraging, and socialising activities, which are

Table 3
Z-test results for statistically significant transitions between the 5 behaviours (Table 1) and under the 4 different contexts (E1 to E2: App-Leave in early years, L1 to L2: App-Leave in late years, E1 to L1: App-App between early and late years, E2 to L2: Leave-Leave between early and late years). The values in bold refer to significant increases, all remaining are decreases.

	E1 to E2		E1 to L1		E2 to L2		L1 to L2	
Transitions	p	Z-value	p	Z-value	p	Z-value	p	Z-value
T -T	**<0.0001**	**8,5**			**0.0018**	**3,1**	**<0.0001**	**11,7**
T - R					0.005	2,8	0.0014	3,2
T - S	<0.001	9,1						
R - T	**<0,0001**	**3,9**			0.,0006	3,4		
R - R			**0.0005**	**3,5**	**<0.0001**	**6,3**		
R - S	0.0002	3,7	0.0002	3,7				
M - T	**<0.0001**	**4,3**						
M - S	0.0002	3,7						
F - T	**<0.0001**	**4,4**					**<0.0001**	**5**
F - F	**0.039**	**2,1**						
F - S								
S - T	**<0.001**	**9,3**			**<0.0001**	**4,7**	**<0.0001**	**10,3**
S - R			0.002	3,1	<0.0001	4,4		
S - S	<0.001	8,4	**<0.0001**	**4,2**	0.0015	3,2	<0.0001	11,7

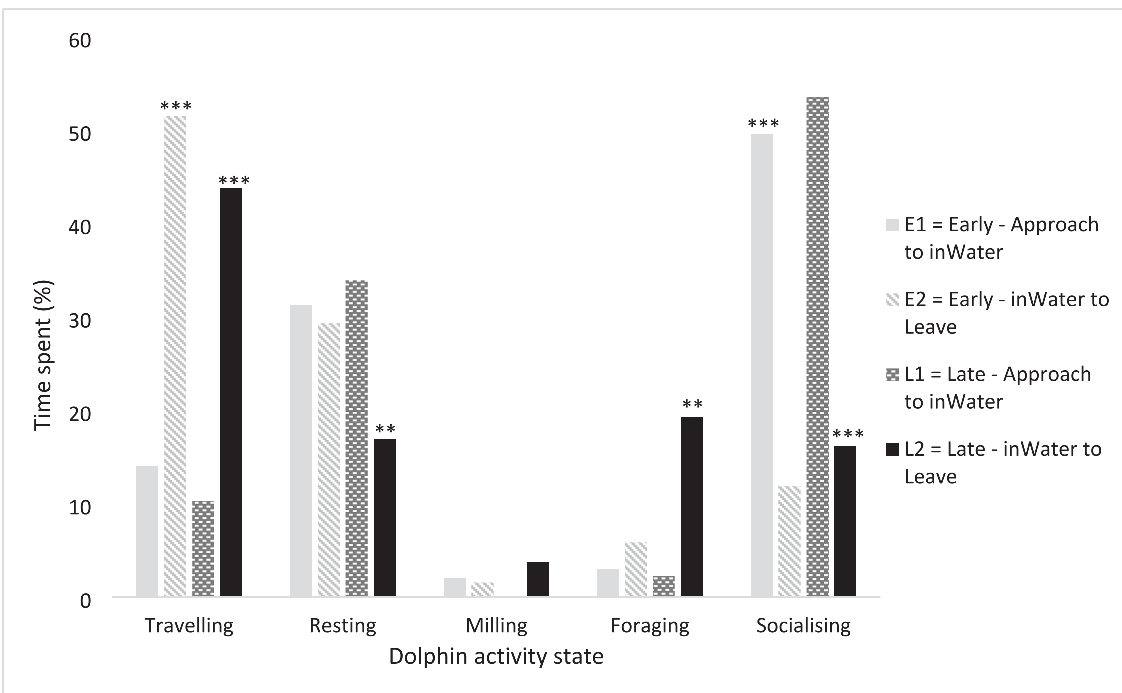

Fig. 6. Behavioural budgets of dolphins in four different time contexts (early years: 2007–2009 – approach to in water, early years: 2007–2009 – in-water to leave, late years: 2017–2019 – approach to in-water, late years: 2017–2019 – in-water to leave). *Z*-Test comparisons results are presented: <0.001 ***; <0.01 **; <0.05 *.

fundamental in physiological terms, may affect the health of individuals and their reproductive success, thus leading to a population decline as reported in other studies (Christiansen et al., 2010; Constantine et al., 2004). Bejder et al. (2006) reported that an increase in the number of permits by even one tour vessel led to significant impacts on the bottlenose dolphin population of Shark Bay, Australia. The present study shows similar results; while comparing the early years when there was only one SWD operator short-term effects appear lower than in the late years where there were four operators.

It is also to note that the calving season for this population takes place when the waters are warmer in austral summer (i.e. beginning in November until February/March), resulting in an overlap between calving season and peak tourism season. In December, each SWD operator conducts on average 3 to 4 trips per day. The trips start at 5:30 am and the last one ends at around 3:00 pm, approximately, each trip can last up to 2 h, resulting in an estimated 67 % of the daylight hours (5 am to 6 pm) where SWD vessels will be searching or actively engaging with dolphins. Although dolphins can be active both during the day and night, their social interactions are mostly diurnal, resulting in large periods of biologically important time being interrupted by tourism.

Vessel data was also collected from the neighbouring bay, Malongane, but only at a later stage and inconsistently. This bay has a single dive center that provides dolphin swimming, ocean safaris, and diving activities. However, given that there are four SWD operators in the reserve and that two launch from Ponta do Ouro bay, future research including all bays where SWD occurs is recommended to obtain a more accurate picture of anthropogenic effects to the dolphin population.

Transition analyses using Markov chains found that SWD activities significantly affected all five of the behavioural states analysed. After tourist swims, dolphins were more likely to travel and less likely to socialise, rest, or forage; similar to the studies of Christiansen et al. (2010) and Lusseau (2003). However, in the early years, dolphins were likely to remain in their preceding behaviour if they were resting, travelling, and foraging. For later years this only occurred if they were travelling.

Most previous studies indicated that dolphin populations disturbed by tourist vessels spent less time foraging (Bejder and Samuels, 2003; Cecchetti et al., 2018; Christiansen et al., 2010; Dans et al., 2008; Lusseau and Higham, 2004; Steckenreuter et al., 2012a, 2012b). This is a biologically significant activity and reducing the energy intake can pose risk to individual and population health (Christiansen and Lusseau, 2013). Due to their small size and active swimming habits, dolphins are required to cover high metabolic costs (Cecchetti et al., 2018). However, in this study we observed a significant increase in time spent foraging, especially in the late years (2 % to 19 %). This increase in foraging could be an attempt to compensate for the significant increase in time spent travelling (early years: 14 % to 51 %; late years: 10 % to 44 %). Increased travelling preceding SWD activities has been documented in several studies (Christiansen et al., 2010; Lusseau, 2003; Steckenreuter et al., 2012a, 2012b), as well as increased travel speeds in the presence of high levels of vessel traffic (Marley, 2017). The increased time and intensity of travelling behaviour would likely result in higher energetic demands, and subsequently reduced fitness at both an individual and population level (Lusseau et al., 2006). Thus, dolphins may attempt to offset this cost through more time spent foraging.

A decrease in resting bouts was also observed; this was most significant for the late years (34 % to 17 %) and is comparable to other similar studies (Cecchetti et al., 2018; Christiansen et al., 2010; Lusseau, 2003; Meissner et al., 2015; Pérez-Jorge et al., 2017b; Steckenreuter et al., 2012a, 2012b). As females nurse during resting periods, a reduction of resting could have serious implications for nursing behaviour (Stensland and Berggren, 2007). Studies have also shown that a reduction of the resting state could induce physiological stress, increase heart rate, and inflate energetic costs, thus reducing energy reserves (Constantine et al., 2004). Low energy reserves could also lead to higher predation risks due to reduced alertness (Christiansen et al., 2010).

Dolphins also spent significantly less time socialising after SWD activities (Christiansen et al., 2010; Dans et al., 2008; Lusseau, 2003; Steckenreuter et al., 2012a, 2012b). Socialising includes mating activities; less time mating can result in a reduction of the reproductive success of the population. Mother-calf interaction is also represented in socialising, these are times when mothers will teach their offspring survival skills, a reduction of this bout could result in unprepared subadults, thus affecting their health and survival rate, resulting in population decline (Senigaglia et al., 2022).

Given the population's size and lack of knowledge about their reproductive rates, it is recommended that continued behavioural monitoring, population estimates, and reproductive success analyses are undertaken (Rocha et al., 2020; Shawky et al., 2020). This is particularly important given that a decline of abundance in a small resident dolphin population could have strong consequences to the long-term sustainability of the population and consequently, to the local SWD industry. When considering small resident populations in busy tourist locations, management strategies may need to be stricter (Allen et al., 2007; Bejder et al., 2006). It is critical that management strategies and national policies be science-based (Christiansen and Lusseau, 2013; Pérez-Jorge et al., 2017b) and that the precautionary approach be implemented through speed restrictions and area closures for all vessels within the PPMR (Rocha et al., 2020; Steckenreuter et al., 2012a, 2012b). Hoyt (2012) suggests closing a third of marine mammal's habitat for a third of daylight hours, as a precautionary measure.

Furthermore, a recent study in the PPMR indicated that the operators have a good grasp of the CoC and that compliance levels should be high (Rocha et al., 2020). Nonetheless, surveyed tourists presented low knowledge of the CoC, but were supportive of such regulations (Rocha et al., 2020). A good solution to increase tourist awareness is to ensure that guides and all staff are trained to disseminate the correct information. A guide training workshop with SWD staff within the PPMR reported significant knowledge gaps; conversely, all participants presented substantial improvements at conclusion (Rocha et al., 2022). Thus, it is recommended that annual compulsory training programmes take place for all staff of SWD operations (Filby et al., 2017a; Rocha et al., 2020; Stensland and Berggren, 2007); this would improve service quality (guide talk, customer service to maximise tourist satisfaction) (Lück, 2015; Weiler and Ham, 2002), as well as ensure that the crews know how to identify the different behaviours correctly, and comply to the CoC to minimise negative impacts on dolphins (Filby et al., 2017a).

The study presented some limitations in the data collection procedures. Group behaviours were not recorded at set time intervals, as most similar studies did. This was not possible given that the platform was a commercial SWD boat during tourism activities. All three observations occurred within a 20-min interval for the late years, as the PPMR regulation only allows for a maximum 20-min disturbance time. However, in the early years there was no time constraint and although there was only one operator, this could remain with the dolphins for up to 1 h. An overall predominant behaviour was recorded for each of the three observations. Another limitation was that in order to have three observations and 2 transitions, the swimmers needed to interact with the dolphins, which was not always possible depending on the dolphin's location and behaviour. If for example, there was a newborn present, the dolphins were swimming fast, or showed aggressive behaviours, then no one was allowed in water and the sighting was excluded from the data set. To compensate for this, we included three early and late years of data to obtain a sufficient sample size.

5. Conclusion

There is a misconception that because dolphins often approach and interact with humans there are no negative consequences. However, these interactions can have long-term detrimental effects on dolphin populations by diverting them from important behaviour such as foraging and resting (Martinez et al., 2011), especially during periods of high tourism intensity (Pérez-Jorge et al., 2017a) which is also the calving and breeding season for this species.

This study has demonstrated that SWD activities have the potential to alter dolphin behaviour to an extent that changes the daily behavioural budget over a period of time. This is important because repeated behavioural disruptions can negatively affect survival and reproduction rates, leading to population-level effects (Tyne et al., 2018).

Additionally, it illustrates the importance of a multidisciplinary adaptive management approach to the PPMR, where management measures are the results of cooperative work between the management of the reserve, researchers, and SWD operators. Where managers make decisions based on information provided by research, and SWD operators comply to implemented measures.

Future growth in commercial tourism activities in the area needs careful consideration by PPMR managers, this is of particular importance when considering the relatively small size of this population. For that reason, continued monitoring of population size and distribution range are needed to better understand its current status.

We urge authorities to strictly regulate present operations along the Mozambican coast and islands, advise against further development of SWD tourism and recommend that any unregulated increase in SWD tourism should be discouraged (Fumagalli et al., 2018).

The study of small resident populations of cetaceans is relevant not only regionally but globally, as small populations contribute to overall population numbers (Steckenreuter et al., 2012a, 2012b).

For that reason, the results presented here have implications for other SWD industries elsewhere and strongly recommend managers to adopt a precautionary approach and make use of lessons learned in well-documented sites worldwide.

CRediT authorship contribution statement

Category 1

Conception and design of study: Diana Rocha; Sarah Marley
acquisition of data: Diana Rocha; Angie Gullan
analysis and/or interpretation of data: Diana Rocha; Sarah Marley
Category 2
Drafting the manuscript: Diana Rocha
revising the manuscript critically for important intellectual content: Sarah Marley; Ben Drakeford; Jonathan Potts
Category 3
Approval of the version of the manuscript to be published: Diana Rocha; Sarah Marley; Ben Drakeford; Jonathan Potts; Angie Gullan

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Allen, S., Smith, H., Waples, K., Harcourt, R., 2007. The voluntary code of conduct for dolphin watching in Port Stephens, Australia: is self-regulation an effective management tool? Cetacean Res.Manag. 159–166.
Bas, A.A., Christiansen, F., Öztürk, B., Öztürk, A.A., Erdoğan, M.A., Watson, L.J., 2017. Marine vessels alter the behaviour of bottlenose dolphins Tursiops truncatus in the Istanbul Strait, Turkey. Endanger. Species Res. 34, 1–14. https://doi.org/10.3354/esr00836.
Bejder, L., Samuels, A., 2003. Evaluating the effects of nature-based tourism on cetaceans. In: Marine Mammals: Fisheries, Tourism and Management Issues. CSIRO Publishing, pp. 229–256.
Bejder, L., Dawson, S.M., Harraway, J.A., 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise bay,New Zealand. Mar. Mamm. Sci. 15 (3), 738–750. https://doi.org/10.1111/j.1748-7692.1999.tb00840.x.
Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., Krützen, M., 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conserv. Biol. 20 (6), 1791–1798. https://doi.org/10.1111/j.1523-1739.2006.00540.x.
Cecchetti, A., Stockin, K.A., Gordon, J., Azevedo, J.M.N., 2018. Short-term effects of tourism on the behaviour of common dolphins (Delphinus delphis) in the Azores. J. Mar. Biol. Assoc. U. K. 98 (5), 1187–1196. https://doi.org/10.1017/S0025315417000674.
Christiansen, F., Lusseau, D., 2013. Understanding the ecological effects of whale-watching on cetaceans. In: Whale-Watching: Sustainable Tourism and Ecological Management, pp. 177–192. https://doi.org/10.1017/CBO9781139018166.016.
Christiansen, F., Lusseau, D., Stensland, E., Berggren, P., 2010. In: Effects of Tourist Boats on the Behaviour of Indo-Pacific Bottlenose Dolphins Off the South Coast of Zanzibar, 11, pp. 91–99. https://doi.org/10.3354/esr00265.
Cisneros-Montemayor, A.M., Sumaila, U.R., Kaschner, K., Pauly, D., 2010. The global potential for whale watching. Mar. Policy 34 (6), 1273–1278. https://doi.org/10.1016/j.marpol.2010.05.005.
Constantine, R., 2001. Increased avoidance of swimmers by wild bottlenose dolphins (Tursiops truncatus) due to long-term exposure to swim-with-dolphin tourism. Mar. Mamm.Sci. 17 (4), 689–702. https://doi.org/10.1111/j.1748-7692.2001.tb01293.x.
Constantine, R., Brunton, D.H., Dennis, T., 2004. Dolphin-watching tour boats change bottlenose dolphin (Tursiops truncatus) behaviour. Biol. Conserv. 117 (3), 299–307. https://doi.org/10.1016/j.biocon.2003.12.009.
Daly, C.A.K., Fraser, G., Snowball, J.D., 2015. Willingness to pay for marine-based tourism in the Ponta do Ouro Partial Marine Reserve,Mozambique. Afr. J. Mar. Sci. 37 (1), 33–40. https://doi.org/10.2989/1814232X.2015.1012556.
Dans, S.L., Crespo, E.A., Pedraza, S.N., Degrati, M., Garaffo, G.V., 2008. Dusky dolphin and tourist interaction: effect on diurnal feeding behavior. Mar. Ecol. Prog. Ser. 369 (July 2014), 287–296. https://doi.org/10.3354/meps07629.
DNAC, 2009. Ponta do Ouro Partial Marine Reserve Management Plan (Issue November).
Filby, N.E., Christiansen, F., Scarpaci, C., Stockin, K.A., 2017. Effects of swim-with-dolphin tourism on the behaviour of a threatened species, the Burrunan dolphin Tursiops australis. Endanger. Species Res. 32 (July), 479–490. https://doi.org/10.3354/ESR00826.
Filby, N.E., Stockin, K.A., Scarpaci, C., 2017. Can marine protected areas be developed effectively without baseline data? A case study for Burrunan dolphins (Tursiops australis). Mar. Policy 77 (November 2016), 152–163. https://doi.org/10.1016/j.marpol.2016.12.009.
Fumagalli, M., Slooten, E., Cesario, A., Costa, M., DiSciara, G., Harraway, J., 2018. Behavioural responses of spinner dolphins to human interactions. R. Soc. Open Sci. 5 (4) https://doi.org/10.1098/rsos.172044.
Heiler, J., Elwen, S.H., Kriesell, H.J., Gridley, T., 2016. Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition. Anim. Behav. 117, 167–177. https://doi.org/10.1016/j.anbehav.2016.04.014.
Hoyt, E., 2012. Marine Protected Areas for Whales Dolphins and Porpoises: A World Handbook for Cetacean Habitat Conservation. Taylor & Francis. https://books.google.pt/books?id=CFzFBQAAQBAJ.
Hoyt, E., 2018. Tourism. In: Wursig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), Encyclopedia of Marine Mammals, 3rd ed. Academic Press, pp. 1010–1014. https://doi.org/10.1016/C2015-0-00820-6.
Jacobs, M.H., Harms, M., 2014. Influence of interpretation on conservation intentions of whale tourists. Tour. Manag. 42, 123–131. https://doi.org/10.1016/j.tourman.2013.11.009.
Lück, M., 2015. Education on marine mammal tours - but what do tourists want to learn? Ocean Coast. Manag. 103, 25–33. https://doi.org/10.1016/j.ocecoaman.2014.11.002.
Lucrezi, S., Saayman, M., 2017. Sustainable scuba diving tourism and resource use: perspectives and experiences of operators in Mozambique and Italy. J. Clean. Prod. 168, 632–644. https://doi.org/10.1016/j.jclepro.2017.09.041.
Lucrezi, S., Milanese, M., Markantonatou, V., Cerrano, C., Sarà, A., Palma, M., Saayman, M., 2017. Scuba diving tourism systems and sustainability: perceptions by the scuba diving industry in two marine protected areas. Tour. Manag. 59, 385–403. https://doi.org/10.1016/j.tourman.2016.09.004.
Lundquist, D., Gemmell, N.J., Würsig, B., Markowitz, T., 2013. Dusky dolphin movement patterns: short-term effects of tourism. N. Z. J. Mar. Freshw. Res. 37–41. https://doi.org/10.1080/00288330.2013.778301. January 2015.
Lusseau, D., 2003. Effects of tour boats on the behaviour of bottlenose dolphins: using Markov chains to model anthropogenic impacts. Conserv. Biol. 17 (6), 1785–1793. https://doi.org/10.1111/j.1523-1739.2003.00054.x.
Lusseau, D., Higham, J.E.S., 2004. Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of bottlenose dolphins (Tursiops spp.) in Doubtful Sound, New Zealand. Tour. Manag. 25 (6), 657–667. https://doi.org/10.1016/j.tourman.2003.08.012.
Lusseau, D., Slooten, L., Currey, R.J.C., 2006. Unsustainable dolphin-watching tourism in Fiordland,New Zealand. Tour. Mar. Environ. 3 (2), 173–178. https://doi.org/10.3727/154427306779435184.
Mann, J., 1999. Behavioral sampling methods for cetaceans: a review and critique. Mar. Mamm.Sci. 15 (1), 102–122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x.
Marley, S.A., 2017. Behavioural and Acoustical Responses of Coastal Dolphins to Noisy Environments (Issue January).
Martinez, E., Orams, M.B., Stockin, K.A., 2011. Swimming with an endemic and endangered species: effects of tourism on Hector's dolphins in Akaroa Harbour,New Zealand. Tour. Rev. Int. 14 (2), 99–115. https://doi.org/10.3727/154427211X13044361606379.
Meissner, A.M., Martinez, E., Orams, M.B., Stockin, K.A., 2014. Effects of commercial tourism activities on bottlenose and common dolphin populations in East Coast Bay of Plenty waters. https://core.ac.uk/download/pdf/132419295.pdf.
Meissner, A.M., Christiansen, F., Martinez, E., Pawley, M.D.M., Orams, M.B., Stockin, K. A., 2015. Behavioural effects of tourism on oceanic common dolphins, Delphinus sp., in New Zealand: the effects of Markov analysis variations and current tour operator compliance with regulations. PLoS ONE 10 (1), 1–24. https://doi.org/10.1371/journal.pone.0116962.
Pérez-Jorge, S., Gomes, I., Hayes, K., Corti, G., Louzao, M., Genovart, M., Oro, D., 2016. Effects of nature-based tourism and environmental drivers on the demography of a small dolphin population. Biol. Conserv. 197, 200–208. https://doi.org/10.1016/j.biocon.2016.03.006.
Pérez-Jorge, S., Louzao, M., Oro, D., Pereira, T., Corne, C., Wijtten, Z., Gomes, I., Wambua, J., Christiansen, F., 2017a. Estimating the cumulative effects of the nature-based tourism in a coastal dolphin population from southern Kenya. Deep-Sea Res. Part II: Top.Stud.Oceanogr. 140, 278–289. https://doi.org/10.1016/j.dsr2.2016.08.011.
Pérez-Jorge, S., Louzao, M., Oro, D., Pereira, T., Corne, C., Wijtten, Z., Gomes, I., Wambua, J., Christiansen, F., 2017b. Estimating the cumulative effects of the nature-based tourism in a coastal dolphin population from southern Kenya. Deep-Sea Res. Part II: Top.Stud.Oceanogr. 140, 278–289. https://doi.org/10.1016/j.dsr2.2016.08.011.
Pirotta, E., Harwood, J., Thompson, P.M., New, L., Cheney, B., Arso, M., Hammond, P.S., Donovan, C., Lusseau, D., 2015. Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences. Proc. R. Soc. B Biol. Sci. 282 (1818) https://doi.org/10.1098/rspb.2015.2109.
Pirotta, E., Booth, C.G., Costa, D.P., Fleishman, E., Kraus, S.D., Lusseau, D., Moretti, D., New, L.F., Schick, R.S., Schwarz, L.K., Simmons, S.E., Thomas, L., Tyack, P.L., Weise, M.J., Wells, R.S., Harwood, J., 2018. Understanding the population consequences of disturbance. Ecol.Evol. May, 1–13. https://doi.org/10.1002/ece3.4458.

Rocha, D., Drakeford, B., Marley, S.A., Potts, J., Hale, M., Gullan, A., 2020. Moving towards a sustainable cetacean-based tourism industry – a case study from Mozambique. Mar. Policy 120. https://doi.org/10.1016/j.marpol.2020.104048.

Rocha, D., Marley, S.A., Drakeford, B., Potts, J., Gullan, A., 2022. The benefits of guide training for sustainable cetacean - based tourism in developing countries, case study – Ponta do Ouro Partial Marine Reserve,Mozambique. J. Coast. Conserv. 1–11. https://doi.org/10.1007/s11852-022-00876-1.

Senigaglia, V., Christiansen, F., Bejder, L., Sprogis, K.R., Cantor, M., 2022. Human food provisioning impacts the social environment, home range and fitness of a marine top predator. Anim. Behav. 187, 291–304. https://doi.org/10.1016/j.anbehav.2022.02.005.

Shane, S.H., Wells, R.S., Würsig, B., 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. Mar.Mamm.Sci. 2 (1), 34–63. https://doi.org/10.1111/j.1748-7692.1986.tb00026.x.

Shawky, A.M., Christiansen, F., Ormond, R., 2020. Effects of swim-with-dolphin tourism on the behaviour of spinner dolphins, at Samadai Reef in the Egyptian Red Sea. Aquat. Conserv. Mar. Freshwat. Ecosyst. 30 (7), 1373–1384. https://doi.org/10.1002/aqc.3332.

Sprogis, K.R., Bejder, L., Hanf, D., Christiansen, F., 2020. Behavioural responses of migrating humpback whales to swim-with-whale activities in the Ningaloo Marine Park, Western Australia. J. Exp. Mar. Biol. Ecol. https://doi.org/10.1016/j.jembe.2019.151254.

Steckenreuter, A., Harcourt, R., Möller, L., 2012. Are speed restriction zones an effective management tool for minimising impacts of boats on dolphins in an Australian marine park? Mar. Policy 36 (1), 258–264. https://doi.org/10.1016/j.marpol.2011.05.013.

Steckenreuter, A., Möller, L., Harcourt, R., 2012. How does Australia's largest dolphin-watching industry affect the behaviour of a small and resident population of Indo-Pacific bottlenose dolphins? J. Environ. Manag. 97 (1), 14–21. https://doi.org/10.1016/j.jenvman.2011.11.002.

Steiner, A., 2011. Activity budget of inshore Indo-Pacific bottlenose dolphins (Tursiops aduncus): a critical evaluation of methods and comparison among other populations. Mar.Mamm.Sci. 27 (1), 20–38. https://doi.org/10.1111/j.1748-7692.2010.00388.x.

Stensland, E., Berggren, P., 2007. Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Mar. Ecol. Prog. Ser. 332, 225–234. https://doi.org/10.3354/meps332225.

Stockin, K.A., Lusseau, D., Binedell, V., Wiseman, N., Orams, M.B., 2008. Tourism affects the behavioural budget of the common dolphin Delphinus sp. in the Hauraki Gulf, New Zealand. Mar. Ecol. Prog. Ser. 355, 287–295. https://doi.org/10.3354/meps07386.

Toro et al., n.d.Toro F, Alarcón J, Toro-Barros B, Mallea G, Capella J, Umaran-Young C, Abarca P, n.d.

Tyne, J.A., Loneragan, N.R., Johnston, D.W., Pollock, K.H., Williams, R., Bejder, L., 2016. Evaluating monitoring methods for cetaceans. Biol. Conserv. 201, 252–260. https://doi.org/10.1016/j.biocon.2016.07.024.

Tyne, J.A., Christiansen, F., Heenehan, H.L., Johnston, D.W., Bejder, L., 2018. Chronic exposure of Hawaii Island spinner dolphins (Stenella longirostris) to human activities. R. Soc. Open Sci. 5, 171506 https://doi.org/10.1098/rsos.171506.

Weiler, B., Ham, S.H., 2002. Tour guide training: a model for sustainable capacity building in developing countries. J. Sustain. Tour. 10 (1), 52–69. https://doi.org/10.1080/09669580208667152.

Williams, R., Lusseau, D., Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). Biol. Conserv. 133 (3), 301–311. https://doi.org/10.1016/j.biocon.2006.06.010.