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Long-term responses of Burrunan dolphins (*Tursiops australis*) to swim-with dolphin tourism in Port Phillip Bay, Victoria, Australia: A population at risk

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ABSTRACT

This study investigated Burrunan dolphin responses to dolphin-swim tour vessels across two time periods: 1998–2000 and 2011–2013. A total of 211 dolphin sightings were documented across 306 surveys. Sighting success rate and mean encounter time with dolphins decreased significantly by 12.8% and 8.2 min, respectively, between periods. Approaches that did not contravene regulations elicited highest approach responses by dolphins towards tour vessels, whereas dolphins' responded to illegal approaches most frequently with avoidance. Small groups responded to tour vessels with avoidance significantly more than large groups. Initial dolphin behaviour had a strong effect on dolphin's responses to tour vessels, with resting groups the most likely to exhibit avoidance. Calves were significantly more likely to be present during swims in 2011–2013. Dolphin's responses to tour vessels changed across time, with effect responses (avoidance and approach) increasing significantly as dolphins gained cumulative experience. These dolphins are forced to expend a greater level of time and energy avoiding or approaching boats, shifting from a non-effect response to an effect response. Consequences of this include possible decrease in biological fitness by detracting from core biological activities such as foraging and resting. Combined with a decrease in sighting success between periods, the results imply that this population of dolphins, which is endemic to Australia and listed as threatened under the Victorian Flora and Fauna Guarantee Act 1988, may not be well suited to the dolphin-swim industry. The management implications of these results warrant a shift from passive to active management in Port Phillip Bay. The importance of long-term research is highlighted, given behavioural responses detected herein would be undetected in short-term studies.

1. Introduction

Human interactions with free-ranging dolphins have the power to improve well-being (Curtin, 2006), enhance participant's values for the targeted species (Orams, 1997), and increase their knowledge levels and pro-conservation actions (Filby et al., in press). Cetacean-based tourism is one of the fastest growing industries worldwide, generating over US$2.1 billion in

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revenue in 2008 (O'Connor et al., 2009) . In Australia more than 1.6 million tourists participate each year, generating over $29 million to the Australian economy, with a high growth rate of 8.3% per annum between 1998 and 2008 (O'Connor et al., 2009).

There is an underlying assumption that if dolphins choose to interact with tour vessels that there will be no detrimental effects. However, dolphin interactions with tour vessels can generate changes in dolphin: respiration patterns (Nowacek et al., 2001); swimming direction (Lemon et al., 2006); swimming speed (Timmel et al., 2008); diving times (Lusseau, 2003); phonation rates (Sousa-Lima and Clark, 2008); behaviour (Peters et al., 2013) and synchrony (Tosi and Ferreira, 2009). How dolphins respond to interactions with tour vessels will depend partly on their age, with calves being more inquisitive and less cautious of vessels, making them more susceptible to impacts (Constantine, 2001; Martinez and Stockin, 2013). Further, research indicates that dolphin's responses to dolphin-swim tour vessels are linked to boat approach type and presence of swimmers and vessels (Bejder et al., 1999; Constantine, 2001; Martinez et al., 2011; Neumann and Orams, 2006; Steckenreuter et al., 2012), with responses varying greatly between the type of tourism undertaken, targeted species and the location (Orams, 2004). These impacts raise concerns relating to the sustainability of this industry (Ziegler et al., 2012); with the limited number of long-term studies indicating short-term behavioural changes can have long-term consequences (e.g., decreased reproductive success (Bejder et al., 2006) and increased mortality rates (Dans et al., 2008) for individuals and their populations (Lusseau and Bejder, 2007)).

Whilst the long-term effects of increasing levels of swim-with dolphin tourism on free-ranging dolphins remain unknown, research suggests that habituation (i.e., a reduction in a behavioural response occurring when a stimulus is frequently repeated with no apparent punishment or reward, Allaby, 1994) often transpires (Constantine, 2001). Tolerance (i.e., no apparent response to a stimulus) is another frequently reported response by animals to human presence (Constantine, 2001), while displacement away from critical habitat has been reported for sensitive individuals (Bejder et al., 2006). Sensitisation may also occur, whereby there is a response increase as the animal learns that the stimulus does have significant consequences (Peters et al., 2013).

The population of dolphins in Port Phillip Bay (hereafter PPB) have recently been identified as a genetically and morphologically isolated species of bottlenose dolphin; the Burrunan dolphin (*Tursiops australis*, Charlton-Robb et al., 2011). Burrunan dolphins are endemic to Australia, with only two resident populations identified: one in PPB and the other in Gippsland Lakes, Victoria. Burrunan dolphins in PPB display high site fidelity, using the southern coastal waters all year round, bringing them into frequent contact with humans (Scarpaci et al., 2003, 2000). Under the Victorian Flora and Fauna Guarantee Act 1988 this population is listed as threatened, and is considered vulnerable to extinction due to its small size (approximately 120 individuals), genetic distinctiveness (Charlton-Robb et al., 2011), restricted home range (which is in close proximity to a major urban centre, making them susceptible to numerous anthropogenic threats) (Hale, 2002), and female natal philopatry (Hale, 2002). Further, this population is at risk due to the considerable volume of vessel activity in the area (commercial and recreational vessels, (Dunn et al., 2001)), and exposure to a non-compliant commercial dolphin-swim industry (Filby et al., in press; Scarpaci et al., 2004).

The dolphin-swim industry in PPB began in 1986 (Jarvis and Ingleton, 2001). In 1995, a code of practice (COP) was established by tour operators and the Department of Conservation and Natural Resources to provide guidelines for responsible behaviour of tour boats around dolphins in PPB. This COP then formed the basis for the Wildlife (Whales) Regulations (1998), with regulations specific to the dolphin-swim tour industry. In order to increase tour operator compliance and improve overall protection of the targeted species (Hale, 2002), these regulations have been amended repeatedly over time to ensure industry sustainability (Scarpaci et al., 2004). In PPB there are currently 3 swim-with dolphin licenced tour operators, entailing 4 vessels, which run a maximum number of 2 trips per day per vessel.

Whilst numerous studies have examined and detected short-term behavioural changes of dolphins in response to tourism activities, few have utilised long-term methodologies to assess potential changes over extended time periods. Given the longevity of marine mammals and the changes that occur within the management of the dolphin-swim tourism industry over time, long-term studies are imperative. This is especially so when dealing with endemic, threatened species upon which an entire commercial industry is based. Herein, a novel long-term assessment approach was used to assess changes in dolphin behaviour over a 15 year period. The aim of this study was to investigate Burrunan dolphins' responses to dolphin-swim tour vessels in PPB across time, in an attempt to detect temporal changes in dolphins' responses to tour vessels and determine how those changes may influence the population's reproduction, survival or population growth in the long-term. In particular, we assess whether the population shows any signs of habituation, sensitisation or tolerance to the dolphin-swim tour vessels with cumulative experience. Furthermore, boat approach type was examined to determine if dolphin's responses differ depending on legality of approach, to determine the effectiveness of the regulations that dictate how tour vessels approach dolphins. Last, we examine if there is a relationship between dolphin's responses to tour vessels based on their age class or their initial behavioural state.

2. Materials and Methods

2.1. Field methods

This study was conducted on the population of free-ranging Burrunan dolphins that inhabit PPB (38°05′S, 144°50′E). Observations of dolphin's responses to tour vessels were conducted on-board dolphin-swim tour vessels that operate in the southern end of PPB across two time frames: (i) period 1 (hereafter P1, 1998–2000, primary researcher: CS); and (ii) period 2

(henceforth P2, 2011–2013, primary researcher: NF). P2 data collection followed methods utilised in P1 for consistency and to enable comparison of results. In some instances, P1 and P2 data were amalgamated to give a long-term data set (hereafter, LTDS).

Dolphins observed in apparent association, moving in the same direction and usually engaged in the same activity were defined as a group (Shane, 1990). The perimeter of the group was established through the use of a 10 m-chain rule between members (Smolker et al., 1992). Tour vessels conducted swims with groups containing animals of all age class: (i) adult (i.e., apparently fully grown individuals (>2 m (range 2.27–2.78 m, Charlton-Robb et al., 2011))) ; (ii) juvenile (i.e., approximately two-thirds the length of an adult and not travelling in the echelon position alongside an adult); (iii) calf (i.e., approximately half the length of an adult, and still travelling in the echelon position alongside an adult, presumed to be its mother); and (iv) neonate (i.e., young calves still showing foetal folds, a floppy dorsal fin, exhibit extreme buoyancy, when surfacing lift the whole head above water and always positioned in close relation to an adult (presumed to be its mother)).

Dolphins' initial behavioural state was recorded as: (i) travelling (dolphins engaged in persistent, directional movement making noticeable headway along a specific compass bearing); (ii) foraging (dolphins involved in any effort to pursue, capture and/or consume prey); (iii) milling (dolphins exhibited non-directional movement, and frequent changes in bearing prevented dolphins from making headway in any specific direction); (iv) resting (dolphins observed in a tight group (<1 body length between individuals), engaged in slow manoeuvres with little evidence of forward propulsion); (v) socialising (dolphins observed chasing, copulating and/or engaged in any other physical contact with other dolphins, such as rubbing and touching) (Filby et al., 2013).

The dolphins' responses to tour vessels were defined as: (i) approach (i.e., >50% of the group changed their behaviour and approached the tour vessel, repeatedly interacting with the vessel and/or swimmers); (ii) neutral (i.e., no apparent change in dolphin's behaviour); and (iii) avoid (i.e., >50% of the group changed their behaviour, changing their direction of travel away from the tour vessel or diving and surfacing away from the tour vessel) (Constantine, 2001).

Tour operators used three approach types to approach dolphin groups, with definitions modified from Scarpaci et al. (2003): (i) parallel (i.e., tour vessel positioned to either side of a group—legal); (ii) direct (i.e., tour vessel positioned directly into the middle of a group—illegal); and (iii) J (i.e., tour vessel initially travelled parallel to a group, but then moved directly in front of the group—illegal). Proportion of approach types used for dolphin encounters was determined by dividing the total number of each approach type observed by the total number of approaches recorded for that encounter.

One minute scan samples were used to collect data on dolphin's responses to tour vessels approaches, number of boats and dolphin's group size, composition and behaviour (Altmann, 1974). Tour vessel approach types and number of approaches per sighting were recorded via continuous observations. Once an approach was recorded, responses of the focal group were correlated to determine the influence of approach type on dolphin response.

Tour duration was deemed as the time the tour vessel departed from dock for the purpose of conducting a dolphin-swim tour until the time the vessel returned to dock. Encounter time was defined as the time the tour vessel was within 300 m of the focal group. Distance (metres) between the tour vessel and the focal group was calculated using a Yardage Pro 500 range finder. Sighting success rate was defined as observing at least one dolphin group per trip, and calculated by dividing the number of trips where at least one dolphin group was observed by the total number of trips conducted. Swim length was calculated as the time (seconds) between the first swimmer entering the water and the last swimmer reboarding the tour vessel.

2.2. Statistical analysis

Statistical analysis was conducted using SPSS 20. All continuous data were tested for normality and homoscedasticity using Anderson–Darling and Bartlett's and Levene's tests, respectively. For the purpose of analyses, group composition was categorised and analysed as either calves absent or calves present. Dolphin's responses were further categorised as: (i) effect (comprised of approach and avoid responses); and (ii) non-effect (consisting of neutral responses). Based on a natural split in the data, group size was categorised as small (1–9 animals) or large (>10 animals). Results were considered statistically significant at $p \leq 0.05$.

Independent samples t-tests were used to determine if there was a significant difference between legal and illegal approaches for: number of approaches used; group size; or number of boats present during an encounter. Differences between P1 and P2 for group size, encounter time, swim length, proportion of parallel approaches, proportion of J approaches and proportion of direct approaches were also assessed via independent samples t-tests.

Data from the LTDS were compared using ANOVAs to determine if swim length, tour vessel's approach number, the dolphins' group size and number of boats present varied with the legality of the approach type used by tour operators. ANOVAs were also run to establish whether the number of approaches used by tour operators was influenced by the dolphins' initial behavioural state or by the dolphins' response to tour vessels. Tukey's post hoc tests were run to determine where differences existed (Pallant, 2001).

Pearson's chi-squared tests were applied to the LTDS to detect whether there is a relationship between the dolphins' responses to tour vessels and approach type, legality of approach type, dolphins' group size, dolphins' initial behavioural state, and dolphins' group composition. Pearson's chi-squared tests were also run to determine if the proportion of dolphin's responses, effect/non-effect responses, responses to parallel approaches, responses to J approaches, responses to direct

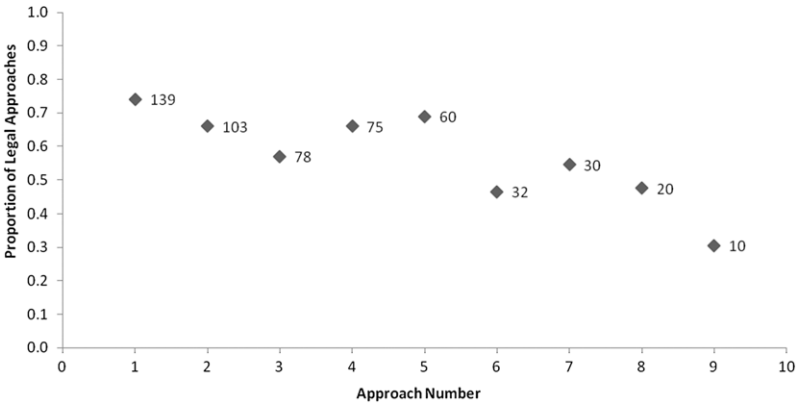

Fig. 1. Proportion of legal approaches towards dolphins made by tour operators for each approach (LTDS).

approaches and sighting success rate differs between P1 and P2. Lastly, Pearson's chi-squared tests were applied to detect whether approach type used by tour operators was influenced by the dolphins' initial behavioural state.

3. Results

Field effort and number of sightings were similar across both periods, with a researcher present on 128 and 178 dolphin-swim trips, respectively during P1 and P2. There were 107 dolphin sightings in P1 (mean tour duration = 3 h 54 min, SD = 28.9 min), and 104 in P2 (mean tour duration = 3 h 22 min, SD = 21.5 min). Sighting success rate decreased significantly ($\chi^2(1) = 4.349$, $p = 0.037$) from P1 (59.4%) to P2 (46.6%). Further, there was a significant ($\chi^2(1) = 4.908$, $p = 0.027$) decrease in sighting success rate within P2, from 58.0% in 2012 down to 37.7% in 2013. There was also a significant difference in mean encounter duration time per sighting between P1 and P2 ($t = 2.531$, $df = 173$, $p = 0.012$). The mean encounter time per sighting decreased from 34.8 min ($n = 107$) in P1 to 26.6 min ($n = 104$) in P2.

Swim length differed significantly between periods ($t = 8.405$, $df = 445$, $p = 0.000$). The mean swim time increased from 170.5 s (SD = 103.7, $n = 331$) in P1 to 262.4 s (SD = 151.4, $n = 263$) in P2. In the LTDS, direct approaches resulted in significantly longer swim times (mean = 239.0 s, SD = 160.6) than J (mean = 204.7 s, SD = 156.0) or parallel approaches (mean = 204.3 s, SD = 121.2) ($F(2, 591) = 3.1$, $p = 0.046$). Tukey's post hoc test identified that direct approaches resulted in significantly longer swims than parallel approaches ($p = 0.039$).

During P1 and P2, a total of 564 and 446 tour vessel approaches were made to dolphin groups, respectively. The mean number of approaches per sighting decreased from 7 in P1 to 4 during P2. Parallel approaches were the most frequently used approach type, in both P1 (63.1%, $n = 440$) and P2 (61.0%, $n = 272$). However, compliance deteriorated across periods, with illegal approaches increasing from 36.9% ($n = 215$) in P1 to 39.0% ($n = 174$) during P2.

The proportion of approaches per sighting for any of the 3 approach types did not vary between P1 (parallel: $n = 107$, mean = 0.695, SD = 0.251; J: $n = 107$, mean = 0.083, SD = 0.147; and direct: $n = 107$, mean = 0.224, SD = 0.235) and P2 (parallel: $n = 96$, mean = 0.691, SD = 0.316, $t = 0.101$, $df = 181$, $p = 0.920$; J: $n = 96$, mean = 0.050, SD = 0.109, $t = 1.812$, $df = 194$, $p = 0.072$; and direct: $n = 96$, mean = 0.259, SD = 0.293, $t = 0.968$, $df = 201$, $p = 0.334$).

For the LTDS, there was a significant difference in boat approach type used by tour operators, depending on the boat approach number ($F(2, 941) = 13.008$, $p = 0.000$, range = 1–21). Tukey's post hoc test revealed that as the number of approaches increased, J approaches (mean = 5.80, SD = 4.310) were significantly more likely to be used than parallel approaches (mean = 4.01, SD = 3.265, $p = 0.000$). Tukey's post hoc test also identified that number of direct approaches (mean = 4.83, SD = 3.837) were significantly higher than number of parallel approaches ($p = 0.006$). A significantly higher number of approaches were used during illegal (mean = 5.10, SD = 3.992) than for legal approaches (mean = 4.01, SD = 3.265) in the LTDS ($t = 4.321$, $df = 630$, $p = 0.000$). The proportion of legal approaches decreased for the LTDS as the number of approaches increased (Fig. 1).

For the LTDS, approach type used by tour operators was significantly influenced by group size ($F(2, 941) = 7.287$, $p = 0.001$). Tukey's post hoc test identified that group sizes for J approaches (mean = 15.01, SD = 15.256, $n = 98$) were significantly larger than for direct (mean = 10.66, SD = 10.102, $n = 255$, $p = 0.002$) or parallel approaches (mean = 10.74, SD = 9.764, $n = 591$, $p = 0.001$). However, there was no significant relationship in the LTDS between legal (mean = 10.74, SD = 9.764) and illegal (mean = 11.87, SD = 11.899) approaches used by tour operators and dolphins' group size ($t = 1.506$, $df = 361$, $p = 0.133$).

In the LTDS, approach type did not vary significantly with the number of boats present ($F(2, 941) = 0.988$, $p = 0.373$), however more boats were present for J approaches (mean = 2.28, SD = 1.470) than for parallel (mean = 2.02, SD = 1.799) or direct approaches (mean = 2.03, SD = 1.489). More boats were present in the LTDS for illegal (mean = 2.10, SD

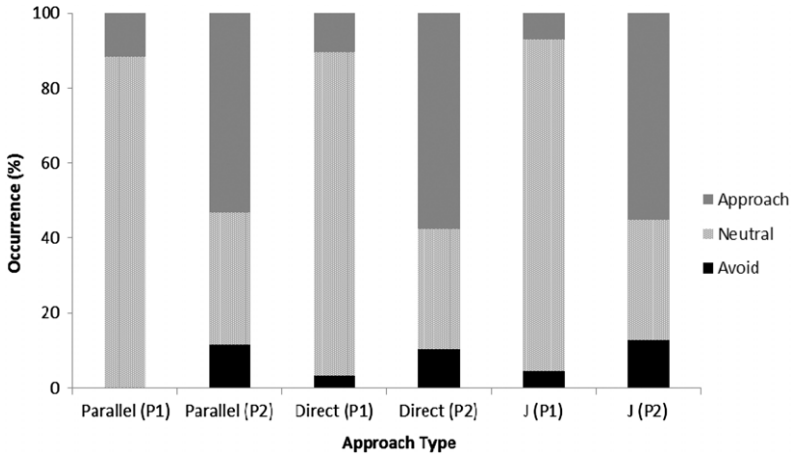

Fig. 2. Dolphin responses to tour vessels as a function of approach type for P1 ($n = 583$) and P2 ($n = 361$).

$= 1.485$) than for legal number of approaches (mean $= 2.02$, SD $= 1.799$), however this result was not significant ($t = 0.669$, $df = 942$, $p = 0.504$).

Approach types used by tour operators did not vary significantly in the LTDS with dolphins' initial behavioural state ($\chi^2(8) = 7.543$, $p = 0.479$). However, the number of approaches made by tour vessels In the LTDS varied significantly with dolphin's initial behavioural state ($F(4, 939) = 5.954$, $p = 0.000$). Tukey's post hoc tests identified that the number of approaches was significantly greater for socialising groups (mean $= 5.53$, SD $= 4.360$) than for travelling (mean $= 4.47$, SD $= 3.587$, $p = 0.041$), foraging (mean $= 3.88$, SD $= 3.307$, $p = 0.004$) or resting groups (mean $= 1.76$, SD $= 1.033$, $p = 0.001$). The number of approaches was also significantly greater for travelling than for resting groups ($p = 0.017$).

3.1. Responses of dolphins to tour vessel approaches

Dolphin responses to tour vessel approaches varied significantly between periods ($\chi^2(2) = 274.863$, $p = 0.000$). Avoidance and approach responses to tour vessels increased from P1 (3.3%, $n = 19$, and 10.8%, $n = 63$, respectively) to P2 (10.0%, $n = 36$, and 56.5%, $n = 204$, respectively), whilst neutral responses decreased from 85.9% ($n = 501$) in P1 to 33.5% ($n = 121$) in P2. Dolphin effect and non-effect responses to tour vessel approaches differed significantly between periods ($\chi^2(1) = 272.548$, $p = 0.000$). Effect responses to tour vessels increased from 14.1% ($n = 82$) in P1 to 66.5% ($n = 240$) in P2, whilst non-effect responses decreased from 85.9% ($n = 501$) in P1 to 33.5% ($n = 121$) in P2.

The dolphins' responses to parallel, J and direct approaches varied between P1 ($n = 583$) and P2 ($n = 361$) ($\chi^2(2) = 191.004$, $p = 0.000$, $\chi^2(2) = 27.886$, $p = 0.000$, and $\chi^2(2) = 62.005$, $p = 0.000$, respectively) (Fig. 2).

For the LTDS, dolphin responses to tour vessel approaches varied significantly with approach type, ($\chi^2(4) = 10.546$, $p = 0.032$), with parallel approaches resulting in the highest approach response (64.8%, $n = 173$). In contrast, when J (8.2%, $n = 22$) or direct approaches (27.0%, $n = 72$) were used, dolphins were less likely to approach. Within approach types, the greatest incidence of avoidance occurred when direct (9.0%, $n = 23$) and J approaches (8.2%, $n = 8$) were used, with parallel approaches resulting in the lowest level of avoidance by dolphins (4.1%, $n = 24$). Dolphins' responses to tour vessels was significantly affected by whether approaches were legal or illegal ($\chi^2(2) = 9.145$, $p = 0.010$). Legal approaches resulted in the highest levels of neutral (63.3%) and approach (64.7%) responses. Conversely, dolphins most frequently responded to illegal approaches with avoidance (56.4%). Approach number also significantly affected dolphin's responses to tour vessels in the LTDS ($F(2, 941) = 4.204$, $p = 0.015$). Dolphins were significantly more likely to approach (mean $= 3.88$, SD $= 3.069$) tour vessels when less approaches were attempted, than to exhibit neutral responses (mean $= 4.64$, SD $= 3.760$, Tukey's post hoc test: $p = 0.011$).

Group size was significantly larger in P2 ($t = 3.113$, $df = 594$, $p = 0.002$, mean $= 13$, SD $= 12.557$, range $= 1$–60) than in P1 (mean $= 10$, SD $= 9.114$, range $= 1$–60). In the LTDS, dolphins' responses to tour vessels varied significantly with group size ($\chi^2(2) = 18.627$, $p = 0.000$). Small groups avoided tour vessels (78.2%, $n = 43$) more frequently than large groups (21.8%, $n = 12$, Fig. 3).

Dolphins' initial behavioural state also had a strong effect on dolphins' responses to tour vessels in the LTDS ($\chi^2(8) = 115.016$, $p = 0.000$). The most frequent response of travelling, foraging and socialising groups was neutral (66.4%, 79.4% and 66.3%, respectively) (Fig. 4). Resting groups most frequently avoid tour vessels (52.9%), approaching tour vessels the least (0.7%). Milling groups most frequently responded to tour vessels by approaching (64.7%). On 64.7% and 20.6% of occasions that tour vessels approached resting or feeding dolphin groups, respectively, they changed their behaviour, exhibiting an effect response.

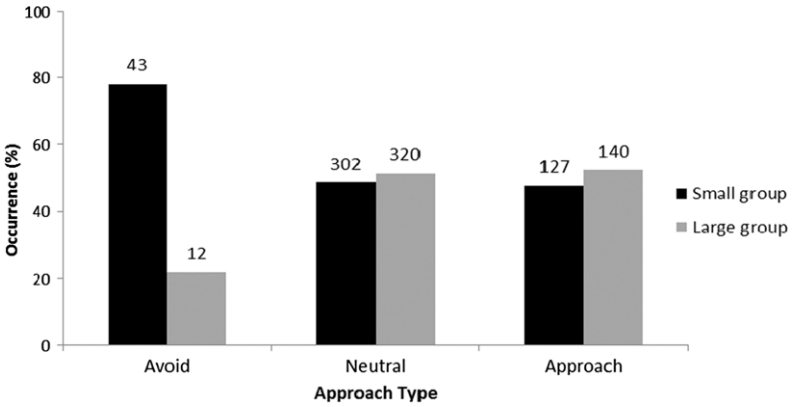

Fig. 3. Dolphin responses to tour vessel approaches as a function of dolphins' group size in Port Phillip Bay, Australia (LTDS). Sample size for each category shown above bars.

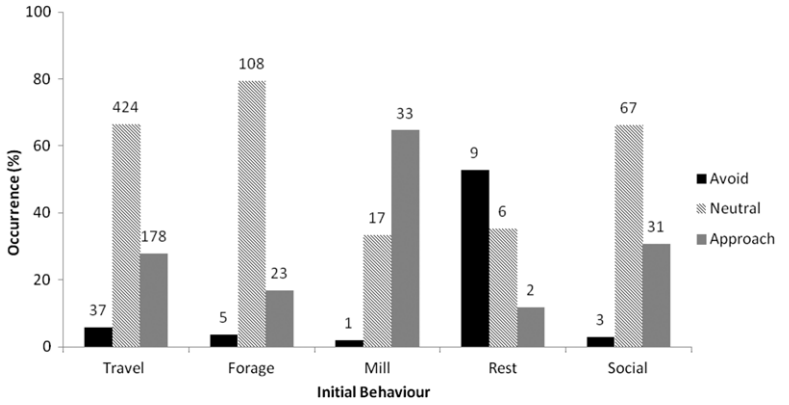

Fig. 4. Dolphin responses to tour vessel approaches in relation to initial behavioural state in Port Phillip Bay, Australia (LTDS). Sample size for each category shown above bars.

3.2. Age composition of dolphins interacting with tour vessels during swims

There was a significant difference in group composition (calves absent vs calves present) between P1 and P2, ($\chi^2(1) = 26.493$, $p = 0.000$), with calves more likely to be present during a swim in P2 (56.9%, $n = 149$) than during P1 (35.1%, $n = 104$). For the LTDS, dolphin responses to tour vessels were significantly affected by group composition ($\chi^2(2) = 16.440$, $p = 0.000$). Dolphins were more likely to avoid (70.9%) or neutrally (58.5%) respond to tour vessels when calves were absent, compared to 29.1% avoidance and 41.5% neutral responses when groups contained calves. Groups with calves present were more likely to approach (53.6%) tour vessels than groups where calves were absent (46.4%) in the LTDS.

4. Discussion

4.1. Responses of Burrunan dolphins to dolphin-swim tour vessels

The findings reported herein reveal that the Burrunan dolphins in PPB have altered their responses to tour vessels across time. Dolphin responses to tour vessels were influenced by the approach type used by tour operators: dolphins approached tour vessels more frequently when legal approaches were used and exhibited higher levels of avoidance to illegal approaches. However, tour operators in PPB are historically non-compliant in utilising legal approaches (Filby et al., in press). Consequently, non-compliance has negative impacts for both the targeted species and the industry, as illegal approaches result in more frequent avoidance responses by the dolphins, which may subsequently decrease both customer viewing opportunities and satisfaction. As the dolphins gained cumulative experience, their responses to tour vessels changed, with dolphins showing an increase in avoidance and approach responses (effect) towards tour vessels across time. These dolphins are forced to expend a greater level of time and energy avoiding or approaching boats, shifting from a non-effect to an effect response, which consequently may decrease their biological fitness (Bejder et al., 1999).

Sighting success rate decreased across time and may reflect a decrease in the number of dolphins using southern PPB. This could possibly be a precursor to abandonment of the bay by the dolphins as the vessel traffic continues to disturb core

biological activities (e.g., feeding and resting, Arcangeli and Crosti, 2009; Christiansen et al., 2010; Constantine et al., 2004; Steckenreuter et al., 2012; Stockin et al., 2008). Potentially, sensitive animals may depart from southern PPB during the tourism period leaving non-sensitive animals, the "risk takers". These "risk takers" are more likely to approach tour vessels, possibly explaining the increase in approach responses to tour vessels from P1 to P2. The increase in approach responses may also be a consequence of bow-riding behaviour, with many delphinid species exhibiting responsive movements towards vessels in order to bow-ride (Filby et al., 2010). However, it is important to recognise that just because these dolphins approach the tour vessels; it does not imply no detriment, long-term consequence (Martinez et al., 2011). These "risk taker" groups that approach tour vessels become the main target foci of the tour operators and as a result, these groups frequently cease their initial behaviour (namely, resting and foraging) in the presence of tour vessels. Consequently, behaviours that are vital to the fitness of the population are being disturbed, and this could potentially lead to long-term population level consequences, as has been reported for other delphinids (Bejder et al., 2006; Higham et al., 2009; Lusseau and Bejder, 2007; Steckenreuter et al., 2012). When resting behaviour is disrupted, the survival of calves is put at risk, as nursing often takes place while animals are resting (Stensland and Berggren, 2007). Further, these "risk taker" groups are at risk of habituation, whereby their responses to stimuli that were once key to their survival progressively wane (Stone and Yoshinaga, 2000) (i.e., over time, they approach vessels more frequently, thereby increasing their risk of vessel strikes).

Alternatively, the dolphins that tour vessels encounter may be "resource dependent" to southern PPB. Scarpaci et al. (2000) identified this region as important for nursery groups given available shelter and productivity. Hence, groups with calves present could be resource dependent to southern PPB and, as a consequence, exposed to frequent encounters with tour vessels. The increase in encounters with groups containing calves from P1 to P2 could be suggestive of this. If this is the case, there is the risk that resource dependent groups may become habituated over time, as they are exposed cumulatively to tour vessels.

In 2012, avoidance levels heightened at 13% possibly due to chronic impacts of dolphin-swim tourism, or alternatively, because of an increase in non-compliance by tour operators to regulations across time (Filby et al., in press). Regardless of what regulatory changes were made, how tour operators approach dolphins has not changed temporally (Filby et al., in press; Scarpaci et al., 2004, 2003). However, how dolphins respond to tour operators has altered over time. Dolphins that approach tour vessels more frequently may have become habituated and be more susceptible to vessel strike, while the increase in avoidance may have resulted in the movement of sensitive animals away from optimal foraging and breeding areas.

Regardless of why dolphins have changed their responses to tour vessels, dolphin groups have decreased their amount of neutral responses to tour vessels across time, meaning that when tour vessels approach, their initial behavioural state changes. This could have significant impacts on the population, given disturbance that interrupts biologically significant behaviours (i.e., resting and feeding) may carry energetic costs that can affect individual fitness and have long-term consequences for the population (Christiansen et al., 2010; Lundquist et al., 2012; Peters et al., 2013).

4.2. Implications from a tour perspective

Between P1 and P2, the quality (sighting success, encounter time and dolphin sightings per trip) of dolphin-swim tours in PPB has deteriorated. This corresponds with an increase in non-compliance (Filby et al., in press) across the same temporal scale, implying that the industry in PPB may be non-sustainable. Dolphins approached tour vessels more frequently when legal (i.e., parallel) as opposed to when illegal (i.e. J and direct) approaches were attempted. Furthermore, legal approaches resulted in the highest levels of neutral responses by dolphins.

The significant increase in swim duration from P1 to P2 indicates that dolphin tolerance to swimmer's presence has increased over time. This may be a consequence of the cumulative exposure dolphins have acquired to the industry. The dolphins studied in P2 have been subject to tourism for a longer period of time and hence may exhibit a higher degree of habituation. Habituation to tourism has been reported for other delphinid species including: Hector's dolphins (*Cephalorhynchus hectori*) in Akaroa, New Zealand (Martinez et al., 2011); dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand (Markowitz et al., 2009); and for Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas (Ransom, 1998). Alternatively, the increase in the mean swim time may reflect amendments made to the regulations between these two periods. In P1, the regulations allowed tour operators an unlimited number of approaches to dolphins; during P2, tour operators were limited to 5 approaches per trip. The limited number of approaches in P2 may be correlated with the longer swim times, as tour operators keep tourists in the water for longer, so that the tour vessel can reposition itself closer to the dolphins. This hypothesis is supported by the increase across time in tour operator's non-compliance to the condition that tour vessels must not reposition the vessel whilst tourists are in the water (Filby et al., in press).

Increased swim length in P2 does not necessarily reflect a satisfactory swim, with tourists in PPB stating that they were not happy with the length of their dolphin-swim (Filby et al., in press). The mean swim time (3.5 min) documented in this study for Burrunan dolphins is low compared to swim times for other species (e.g., 9 min for dusky dolphin (Markowitz et al., 2009), 12 min for rough toothed dolphins (*Steno bredanensis*) in the Canary Islands (Nichols et al., 2002) and 25 min for Hector's dolphins (Martinez et al., 2011)). These findings indicate that Burrunan dolphins, similar to common dolphins (*Delphinus delphis*) in Mercury Bay, New Zealand (mean swim time of 3 min, Neumann and Orams, 2006), may not be receptive to dolphin-swim tourism. Alternatively, the low mean swim time reported for dolphins in PPB may be due to different swim techniques used. Regulations in PPB require tourists to hold onto mermaid lines (these are approximately

15 m long and are streamed from the stern of a vessel) during their dolphin-swim, whereas all of the other dolphin-swims studies compared here use free swims. In PPB, a maximum of 10 people are permitted on to mermaid lines at a time, and every time swimmers swap over, a new short dolphin-swim encounter begins. In comparison, free-swims allow tourists to get in and out of the water with dolphins continuously, and this is counted as one longer dolphin-swim.

4.3. Group size of dolphins interacting with dolphin-swim tour vessels during swims

Small groups of dolphins in PPB avoid tour vessels significantly more frequently than larger groups. Smaller groups may see tour vessels as a potential threat, and hence avoid tour vessels more frequently than larger groups. Delphinids often form larger groups in situations of threat or danger, in an attempt to provide increased vigilance and predator protection via group defence (Gygax, 2002; Zaeschmar et al., 2014). Hence, dolphins travelling in larger groups in PPB may perceive potential threats, such as tour vessels, as less threatening than small groups, explaining the higher approach rate to tour vessels by large groups. The theory that dolphins find safety in numbers is supported by Leitenberger (2001) and Neumann and Orams (2006) who also reported that dolphin group size was significantly correlated with boat avoidance, with smaller groups more likely to avoid vessels than larger groups. Half of dolphin groups encountered in PPB were small (less than 9 animals) and were significantly more likely to avoid tour vessels than larger groups (10 or more animals), adding support to the theory that the population of Burrunan dolphins in PPB may not be well suited to the dolphin-swim tourism industry.

4.4. Age class of dolphins interacting with dolphin-swim tour vessels during swims

Groups containing calves were more likely to be present during dolphin-swims in P2 than in P1. Simultaneously, tour operators' compliance to the condition in the regulations "must not swim with calves" decreased by 14.3% across this time frame (Filby et al., in press). Hence, the greater number of calves observed during dolphin-swims in P2 may reflect tour operators approaching groups with calves present more frequently than in P1, rather than these groups responding by approaching vessels. Potentially, tour operators may swim with groups containing calves more frequently in P2 by necessity. The significant decrease in sighting success across time will conceivably increase pressure on tour operators to swim with the first group they encounter in P2, regardless of age class composition. Potentially, groups containing calves may respond to tour vessels by approaching and bow-riding because of their inability to manoeuvre rapidly enough or dive sufficiently to avoid tour vessels (Wells and Scott, 1997). However, this approach response by groups containing calves may increase calves' susceptibility to disturbance by approaching vessels.

The significant increase of groups containing calves interacting with tour vessels during dolphin-swims across time is of concern, as neonates and calves are particularly vulnerable to collisions with vessels (Dwyer et al., 2014; Laist et al., 2001; Martinez and Stockin, 2013; Stone and Yoshinaga, 2000). Dolphins in P2 have been repeatedly exposed to tourism and thus may be displaying long-term behavioural changes such as habituation, which could lead to an increase in accidental encounters (Hawkins and Gartside, 2008). Habituated dolphins may display reduced wariness and let their calves interact with tour vessels more closely and frequently than non-habituated individuals (Bejder and Samuels, 2003). Consequently, these individuals become more vulnerable to vessel strike, especially calves due to their inexperience and reduced capacity to avoid vessels (Laist et al., 2001; Martinez and Stockin, 2013; Wells and Scott, 1997). Furthermore, vessels that get too close to dolphins groups can interrupt the nursing behaviour of young calves, which may cause disruption to social behaviours (Samuels et al., 2003; Wells et al., 2008).

PPB is an important area for breeding for this small population of Burrunan dolphins that is listed as threatened, with as many as six calves born in the austral summer of 2012–2013 (Filby, unpubl. data). However, there is a history of calf mortality due to vessel strike in PPB (Warren-Smith and Dunn, 2006). Given high levels of non-compliance (Filby et al., in press; Scarpaci et al., 2004, 2003) and the significant increase in effect responses to tour vessels by dolphins reported herein, there warrants a shift from passive (i.e., minimal enforcement presence and reliance on outreach material) to active (i.e., officers policing waters within PPB on a daily basis and sanctioning fines for breaches of regulations/ loss of permits for multiple breaches) management in PPB. If active management cannot be implemented due to resource limitations, then the authors suggest that the dolphin tourism industry be questioned since it may not be suitable for this particular population in PPB.

5. Conclusions

Burrunan dolphins in PPB have altered their responses to tour vessels across time, with dolphins showing an increase in effect responses towards tour vessels across 15 years. Combined with a decrease in sighting success, these results suggest that the population of dolphins in PPB is not well suited to the dolphin-swim industry. Management of the industry must consider not only how to regulate and enforce how tour vessels approach dolphins, but also how dolphins respond to tour vessels, as even seemingly positive encounters could have deleterious long-term effects on the population by detracting from biologically significant behaviours such as foraging, nursing and resting. This study highlights the importance of long-term data sets, as the results from either period alone are insufficient to give an indication of the impacts the dolphin-swim industry has on this population. However, by examining the short-term comparative studies concurrently, we gain valuable insight into behavioural changes that have occurred over time, and have detected responses resembling habituation.

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