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Filby, Nicole E, Christiansen, F, Scarpaci, Carol and Stockin, KA (2017) Effects of swim-with-dolphin tourism on the behaviour of a threatened species, the Burrunan dolphin Tursiops Australis. Endangered Species Research, 32. pp. 479-490. ISSN 1863-5407

Vol. 32: 479–490, 2017
https://doi.org/10.3354/esr00826

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published June 15

Effects of swim-with-dolphin tourism on the behaviour of a threatened species, the Burrunan dolphin *Tursiops australis*

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ABSTRACT: Burrunan dolphins *Tursiops australis* are frequently targeted by tourism operations in Port Phillip Bay, Australia. This study aimed to provide first insights into whether swim-with-dolphin (SWD) vessels in Port Phillip Bay affect the behaviour of Burrunan dolphins via the use of Markov chain models. The presence of SWD vessels affected dolphins' travelling, foraging, milling and socialising behaviours. The time dolphins spent foraging in the presence of SWD vessels was significantly reduced, with average foraging bout length decreasing by 13.6%, foraging recovery time increasing by 47.6%, and the probability of transitioning from foraging to milling increasing 4-fold. Conversely, dolphins spent significantly more time milling and socialising in the presence of SWD vessels. The reduction in time spent foraging when SWD vessels are present could lead to a decrease in dolphins' rate of energy acquisition, whilst the increase in milling could increase their energy expenditure. Collectively, this may lead to reduced biological fitness with population level consequences. However, although the short-term behavioural budget of the dolphin population was significantly affected, SWD vessels did not significantly affect the cumulative (i.e. yearly) behavioural budget of Burrunan dolphins. Thus, the assumption that boat-based cetacean tourism has major negative effects on targeted populations may be flawed in some cases.

KEY WORDS: Tourism impact · Markov chains · Behavioural budget · Vessel exposure · Foraging · Disturbance · Management · Australia

INTRODUCTION

Cetacean-based tourism is one of the fastest growing global industries, occurring in over 119 countries (Hoyt 2001). It is the largest current economic activity dependent upon cetaceans (Parsons 2012), with over US$2.1 billion generated in revenue worldwide in 2008 (O'Connor et al. 2009). In Australia, more than 1.6 million tourists participate annually, contributing over US$31 million to the Australian economy (O'Connor et al. 2009). Within Victoria, cetacean tourism generates over US$871 554 annually (O'Connor et al. 2009). These human interactions with cetaceans have the potential to increase participants' knowledge levels and pro-conservation actions (Stamation et al. 2007, Filby et al. 2015) and enhance participants' values for the targeted species (Orams 1997). Further, whale watching is an economically viable alternative to whaling (O'Connor et al. 2009). However, the rapid expansion of this industry has raised concerns over impacts on the targeted species (e.g. IWC 2006, Lusseau & Bejder 2007, Higham et al. 2014, Christiansen & Lusseau 2015).

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Short-term responses of cetaceans to boat-based tourism include changes in behaviour (Lusseau et al. 2009, Steckenreuter et al. 2012, Christiansen et al. 2013, Meissner et al. 2015), swim speed and direction (Nowacek et al. 2001, Timmel et al. 2008, Christiansen et al. 2014), respiration and dive characteristics (Janik & Thompson 1996, Lusseau 2003b, Ng & Leung 2003, Richter et al. 2006), group cohesion (Bejder et al. 1999, Hastie et al. 2003, Tosi & Ferreira 2009), communication (Scarpaci et al. 2000a) and habitat use (Bejder et al. 1999, 2006a, Courbis & Timmel 2009). These impacts raise concerns relating to the sustainability of cetacean-based tourism, as short-term behavioural changes can have long-term population consequences (IWC 2006, Christiansen & Lusseau 2015).

Long-term exposure to boat-based tourism may affect cetaceans by increasing stress levels (Romano et al. 2004, Wright et al. 2007, 2009), increasing daily energetic costs (Williams et al. 2006, Christiansen et al. 2013, 2014), causing short-term displacement from important habitats (Bejder et al. 2006b) and/or decreasing reproductive success (Bejder 2005). However, responses vary greatly depending on the target species, the type of tourism undertaken and the location (Orams 2004, Senigaglia et al. 2016). Consequently, for many target species, the severity and extent of long-term impacts are likely underestimated, if at all known. This is of particular concern for endangered species, such as the Burrunan dolphin *Tursiops australis*.

Burrunan dolphins are endemic to Australia and are recognised as 'threatened' under the Victorian Flora and Fauna Guarantee Act (1988). Due to Burrunan dolphins being a newly described species, they are not yet listed on the IUCN Red List but will be listed as Data Deficient. The population of Burrunan dolphins in Port Phillip Bay (PPB) is considered vulnerable to extinction due to its small size (approximately 100 individuals) (Warren-Smith & Dunn 2006, Charlton-Robb et al. 2015), genetic distinctiveness (Charlton-Robb et al. 2011, 2015), restricted home range, female natal philopatry and anthropogenic chemical pollution (e.g. mercury; Monk et al. 2014). This population's vulnerability is further exacerbated by its high site fidelity in the southern coastal waters of PPB (Scarpaci et al. 2000b, 2003, 2004, Warren-Smith & Dunn 2006). This coastal distribution (Charlton-Robb et al. 2011, Filby et al. 2017) increases the risk of exposure to a number of threats, including a non-compliant commercial swim-with-dolphin (SWD) industry (Scarpaci et al. 2004, Filby et al. 2015) and vessel strikes (Dunn et al. 2001) due to the high level of commercial and recreational vessel activity in the bay. Given the aforementioned concerns, the population of Burrunan dolphins in PPB may be especially vulnerable to human disturbance.

The PPB dolphin population has been exposed to commercial SWD tourism since 1986 (Jarvis & Ingleton 2001). Currently, 3 licenced SWD operators, comprising 4 vessels, operate in the region, departing from Sorrento and Queenscliff (Fig. 1). SWD trips operate between October and May annually, with each vessel running a maximum of 2 trips daily. The SWD vessels are generally on the water from 08:30 to 18:00 h. A large number of other commercial and recreational vessels use the bay on a daily basis. On weekends, particularly during the austral summer months, there is a pronounced increase in the number of recreational vessels using PPB (Weir et al. 1996).

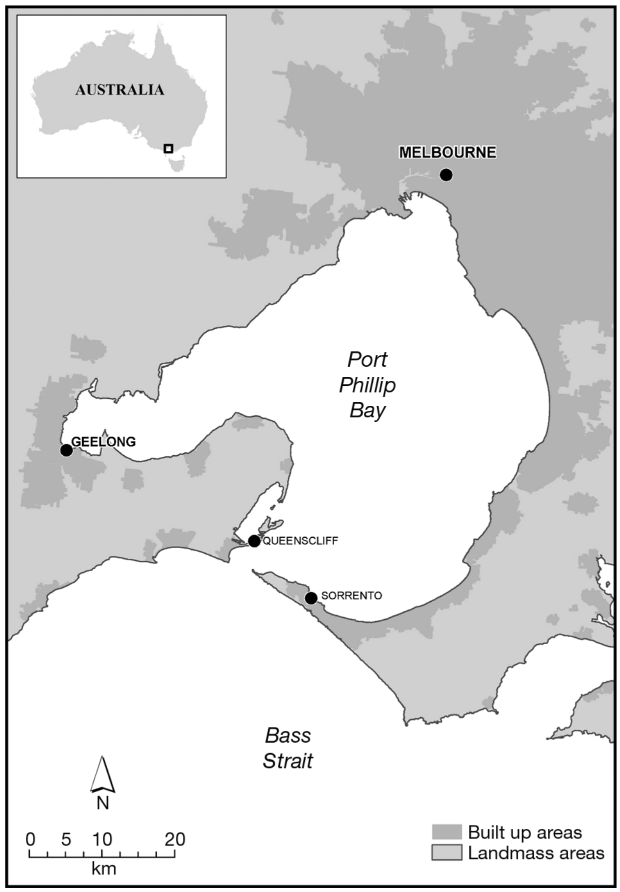

Fig. 1. Port Phillip Bay, Victoria, Australia, depicting Queenscliff and Sorrento, from where the swim-with-dolphin vessels depart. Built up (urban) areas encompass developed areas (i.e. any land on which buildings and/or other structures are present), construction areas and roads. Landmass areas are defined as large, continuous areas of land with no buildings present

Interactions with dolphins in the Australian state of Victoria are governed by the Wildlife (Marine Mammal) Regulations (2009), with specific regulations pertaining to the SWD tourism industry. The Department of Environment, Land, Water and Planning is currently the body responsible for enforcing these regulations. However, the SWD tourism industry in PPB has historically been non-compliant with regulations (Scarpaci et al. 2003, 2004, Filby et al. 2015). This behaviour negatively impacts the dolphins as well as the industry, as dolphins exhibit higher levels of avoidance to illegal approaches but approach SWD vessels more frequently when legal approaches are used (Filby et al. 2014).

Recent research has revealed that the way Burrunan dolphins respond to SWD vessel approaches in PPB has changed over time. Dolphins' responses to SWD vessels were defined as: (1) approach (i.e. >50% of a group approached the SWD vessel, repeatedly interacting with the SWD vessel and/or swimmers); (2) neutral (i.e. no apparent change in the dolphins' behaviour); and (3) avoidance (i.e. >50% of a group changed their direction of travel away from the SWD vessel). Filby et al. (2014) documented significant increases in approach and avoidance responses from 1998 to 2013. Thus, these dolphins likely expend greater levels of time and energy during SWD tourism interactions, with possible missed opportunities for foraging and socialising (including mating, Filby et al. 2014). This is of concern, given recent research indicating that PPB is an important foraging and nursery ground for Burrunan dolphins (Scarpaci et al. 2010, Filby et al. 2017) and that groups containing calves are those most likely to avoid SWD vessels (Filby et al. 2014).

Within the published literature to date, no studies have described the effects of SWD tourism on the behaviour of Burrunan dolphins. Understanding whether tourism activities affect the behavioural budget of the PPB population of Burrunan dolphins is of critical importance, as this threatened population interacts with a non-compliant SWD industry that operates intensively across summer months when calves are most frequently observed (Filby 2016).

The aim of this study was to assess the short-term effects of SWD vessels on the behaviour of Burrunan dolphins in PPB. Using Markov chain analyses, the effects of tourism on the dolphins' behavioural budget were assessed. Further, we aimed to determine whether disturbances caused by the SWD tourism industry affect the long-term behavioural budget of the population, by calculating the cumulative (i.e. yearly) exposure of Burrunan dolphins to SWD activities in PPB. Findings are discussed in a management context to provide tailored recommendations that can be implemented into a management framework for this population.

MATERIALS AND METHODS

Study site

PPB (38° 05′ S, 144° 50′ E) is situated on the southeastern coast of the state of Victoria, Australia, with the major metropolitan cities of Melbourne (37° 48′ 49″ S, 144° 57′ 47″ E) and Geelong (38° 09′ 0″ S, 144° 21′ 0″ E) bordering its coastline (Fig. 1). It is the largest bay in Victoria, covering 1940 km^2. The bay, with a maximum depth of 24 m (mean = 13.6 m), has an oceanic climate, supporting a diverse and dynamic ecosystem, with high biodiversity.

Data collection

From November 2010 to May 2013, surveys documenting the behavioural states of Burrunan dolphin groups in PPB were conducted, using focal-group follows (Altmann 1974). A dolphin group was defined as 2 or more animals in which no individual was farther than 10 m from its nearest conspecific (Smolker et al. 1992). Data were collected from 2 observation platforms: (1) an independent research vessel, the 'Pelagia', a 6.5 m platform, powered by two 100-horsepower, 4-stroke Yamaha engines; and (2) the 'Maureen M', a 10.9 m long SWD vessel, with a 110 horsepower engine. Only data collected during surveys conducted in sea states of Beaufort 3 or less were used in the analysis.

From both observation platforms, the study area was searched non-systematically to locate dolphins. Once dolphins were detected, the research vessel changed to a slow approach speed (~2–4 knots) and manoeuvred towards the group in a consistent manner to minimise disturbance to the dolphins (Lusseau 2003a). Thus, dolphins were always approached from the side and rear (i.e. parallel approach, Scarpaci et al. 2003), with the research vessel moving in the same direction as the dolphin group. Further, rapid changes in speed, shifts of gear and change of course by the research vessel were avoided (Jensen et al. 2009, Christiansen et al. 2010). When conducting a follow, the speed of the research vessel always matched that of the slowest group member, and a distance of 50 m or more from the focal group was always maintained. This protocol was maintained when SWD vessels were present and, thus, the state of the research vessel remained consistent in all control and impact scenarios. Consequently, any differences in observed behaviour would relate only to the presence of the SWD vessel. In contrast, SWD vessels usually approached dolphins at higher speeds and to a much closer range (<5 m). SWD vessels used 3 approach types: (1) J (SWD vessel initially travelled parallel to a group, but then moved directly in front of the group); (2) direct (SWD vessel approached directly into the middle of a group); and (3) parallel (SWD vessel approached to the side of a group; Scarpaci et al. 2003, Filby et al. 2014).

During a focal follow (regardless of the observation platform), the time, behavioural data and presence/absence of SWD vessels were recorded every 3 min using focal-group scan sampling (Altmann 1974). Five behavioural states were identified: travelling, foraging, milling, resting and socialising (Table 1). The predominant behaviour was determined as the behavioural state in which more than 50% of dolphins were involved (Stockin et al. 2008, 2009). These behavioural states were mutually exclusive and, collectively, described the entire behavioural repertoire of the dolphins observed. Burrunan dolphins live in fluid fission-fusion societies where group composition can change daily. Focal follows terminated when the weather deteriorated, animals were lost (10 min elapsed without a sighting) or when daylight hours ended.

Control scenarios were defined as observations where only the research vessel was within 300 m of the focal group (i.e. absence of any other vessels within 300 m of the focal group). Impact scenarios were observations with at least 1 SWD vessel within 300 m of the focal group. This distance of 300 m is consistent with the prescribed minimum distance for vessels approaching dolphins in the Victorian Wildlife (Marine Mammal) Regulations (2009). Distance (m) between the SWD vessel(s) and the focal group was calculated using a Yardage Pro 500 range finder (Bushnell). For analyses, scan samples up to 15 min (5 scan sampling events) after an interaction involving the presence of an SWD vessel within 300 m of the focal group were classified as impact scenarios, whereas scans greater than 15 min after an interaction involving the presence of an SWD vessel were deemed as control scenarios. Observations from the research vessel were used to collect data in both control and impact scenarios, whereas observations from aboard the SWD vessel were used only to collect data from impact scenarios. Due to the small sample size, it was not possible to test the effect of different numbers of SWD vessels on dolphin behaviour.

Effect of SWD vessel interactions

Transition probabilities

Markov chains were used to investigate the effect of SWD vessels on the behaviour of Burrunan dolphins while taking into account the temporal dependence between behavioural states (Lusseau 2003a, Christiansen et al. 2010). A first-order Markov chain was used, which estimates the transition probabilities between preceding and succeeding behavioural states. The time series of behavioural states resulting from each focal follow was first tallied into 2 contingency tables, one for control and one for impact scenarios. From the resulting matrices, the transition probability between the preceding behavioural state and the succeeding behavioural state was estimated (Lusseau 2003a, Christiansen et al. 2010). For calcu-

Table 1. Behavioural states used to assess the behavioural budget of Burrunan dolphins *Tursiops australis* in Port Phillip Bay, Victoria, Australia (modified from Shane et al. 1986, Scarpaci et al. 2010, Filby et al. 2013)

Behavioural state	Definition
Travelling	Consistent and directional movement, making noticeable headway along a specific compass bearing, with short, relatively constant dive intervals
Foraging	Perusal, capture and/or consumption of prey, as defined by observations of 2 or more of the following: erratic movements at the surface; multi-directional diving; coordinated deep diving; fish chasing; and rapid circle swimming. Prey often observed at the surface
Milling	Non-directional movement. Frequent changes in bearing preventing dolphins from making noticeable headway in any specific direction. Individuals surfacing facing various directions
Resting	Low activity level, with surfacing slow and more predictable than those observed in other behavioural states. Tight groups (<1 body length between individuals) observed, with little evidence of forward propulsion
Socialising	Chasing, copulating, petting, rubbing, genital inspections, playing and any other physical contact between individuals. Aerial behaviours such as breaching frequently observed

lations, see the 'Transition probabilities' section in the Supplement at www.int-res.com/articles/suppl/n032p479_supp.pdf.

The overall effect of SWD vessels on the transition probabilities between behavioural states was tested by comparing the control and impact contingency tables, using a chi-squared test. The effect of SWD vessels on each specific transition probability was also examined by comparing each control transition to its corresponding impact transition, using a 2-sample test for equality of proportions with continuity correction.

Behavioural budgets

From the contingency tables, the dolphins' behavioural budgets (i.e. the proportion of time dolphins spend in each behavioural state) were calculated in the presence and absence of SWD vessels, through eigen analysis (see Lusseau 2003a for details of analysis). The control and impact behavioural budgets were then compared using a chi-squared test. In addition, the difference in proportion of each behavioural state in the presence and absence of SWD vessels was compared using 2-sample tests for equality of proportions.

Average bout length

The average bout length (the duration of time [min] that the dolphins spent continuously in each behavioural state) of each behavioural state was calculated in the presence and absence of SWD vessels following Lusseau (2003a). For calculations see the 'Average bout length' section in the Supplement. The average bout length for each behavioural state was compared between control and impact scenarios using a *t*-test.

Recovery time

The average time it took a dolphin group to return to a given behavioural state, i.e. the recovery time, was estimated in the presence and absence of SWD vessels (Stockin et al. 2008). For calculations see the 'Recovery time' section in the Supplement.

SWD vessel exposure

Model simulations were run to estimate the annual exposure of individual dolphins to SWD vessels, based on the daily number of SWD trips throughout the year: winter = 0 trips d^{-1}; spring = 3 trips d^{-1}; summer = 6 trips d^{-1}; and autumn = 4 trips d^{-1}. The number of dolphins in the PPB population was set at 100 (Warren-Smith & Dunn 2006, Charlton-Robb et al. 2015). The yearly frequency, f_d, of interactions with SWD vessels for each individual dolphin, d, was then estimated (Christiansen et al. 2015) as:

$$f_d = \sum_{w=1}^{W} \text{Bernoulli}(E_w) \quad (1)$$

where W is the total number of SWD trips in the year (i.e. 1187) and E is the probability of encountering an individual dolphin d on a given trip w, assumed to be 46.6% (Filby et al. 2014). The cumulative interaction time (min) with SWD vessels throughout the year was then estimated by randomly allocating a duration to each interaction, f_d, based on the distribution of observed encounter durations (mean = 27 min, SD = 17, min = 2, max = 92, n = 104) between SWD vessels and dolphins in PPB, and summing up the result (Christiansen et al. 2015).

Cumulative behavioural budgets

Based on the estimated exposure to SWD vessels throughout the year, the dolphins' cumulative behavioural budget was estimated (Lusseau 2003a, Christiansen et al. 2010). This budget takes into account the proportion of time that dolphins spend with SWD vessels throughout the year. By comparing the cumulative behavioural budget to the dolphins' undisturbed behavioural budget (i.e. their control budget), it is possible to measure the effect of SWD vessel interactions on the dolphins' yearly behavioural budget. The cumulative behavioural budget was estimated following Christiansen et al. (2010) and Lusseau (2003a). For calculations see the 'Cumulative behavioural budgets' section in the Supplement.

All analyses were performed in R 3.0 (R Core Team, 2013).

RESULTS

Field effort

From November 2010 to May 2013, 112 h over 96 d were spent undertaking focal follows. A total of 153 (50 from onboard the research vessel and 103 from onboard the SWD vessel) independent Burrunan dolphin groups were observed. The mean ± SE observation time per group from the research vessel was 80 ± 11.2 min (range = 2–291 min, n = 50), and 27 ± 1.7 min (range = 2–92 min, n = 103) from the SWD vessel. In total, we recorded 1912 behavioural transitions, of which 951 and 961 were control and impact transitions, respectively. Due to the small sample size (n = 65) of transitions involving 'rest', all transitions to and from this behavioural state had to be excluded from the analyses, leaving 923 (50.0%) and 924 (50.0%) behavioural transitions for control and impact scenarios, respectively. These transitions were collected over 47 control and 102 impact sequences. Control sequences (64.3 ± 9.4 min, range = 5–251 min) were on average 35 min longer than impact sequences (29.2 ± 1.8 min, range = 5–89 min).

Effect of SWD vessel interactions

Transition probabilities

SWD vessel interactions significantly affected the dolphins behavioural state transitions (goodness-of-fit test, $\chi^2 = 116.60$, df = 9, $p < 0.001$). However, observed effects were not homogenous amongst all transitions, with 4 transitions being significantly influenced by the presence of SWD vessels (Fig. 2). The transitions, Travelling → Milling ($\chi^2 = 10.06$, $p = 0.002$), Foraging → Milling ($\chi^2 = 4.52$, $p = 0.033$) and Socialising → Socialising ($\chi^2 = 9.17$, $p = 0.002$) all increased significantly when SWD vessels were present. Conversely, the other notable transition, Socialising → Travelling ($\chi^2 = 6.03$, $p = 0.014$), decreased significantly in the presence of SWD vessels. The magnitude of difference in transition probability was not homogenous for all transitions. Dolphins were twice as likely to start milling after being in a travel state (Travelling → Milling: 6.9% → 12.7%) and 4 times more likely to commence milling when originally foraging in the presence of SWD vessels (Foraging → Milling: 2.7%→ 9.7%). Dolphins were 47.1% more likely to remain socialising (Socialising → Socialising: 43.1% → 66.4%) when SWD vessels were present. The probability of travelling after being in a socialising state decreased by 42.9% (Socialising → Travelling: 41.7% → 23.8%) in the presence of SWD vessels (Fig. 2).

Behavioural budgets

The behavioural budget of Burrunan dolphins was significantly affected by the presence of SWD vessels (goodness-of-fit test, $\chi^2 = 46.74$, df = 3, $p < 0.001$; Fig. 3). Dolphins spent significantly more time milling

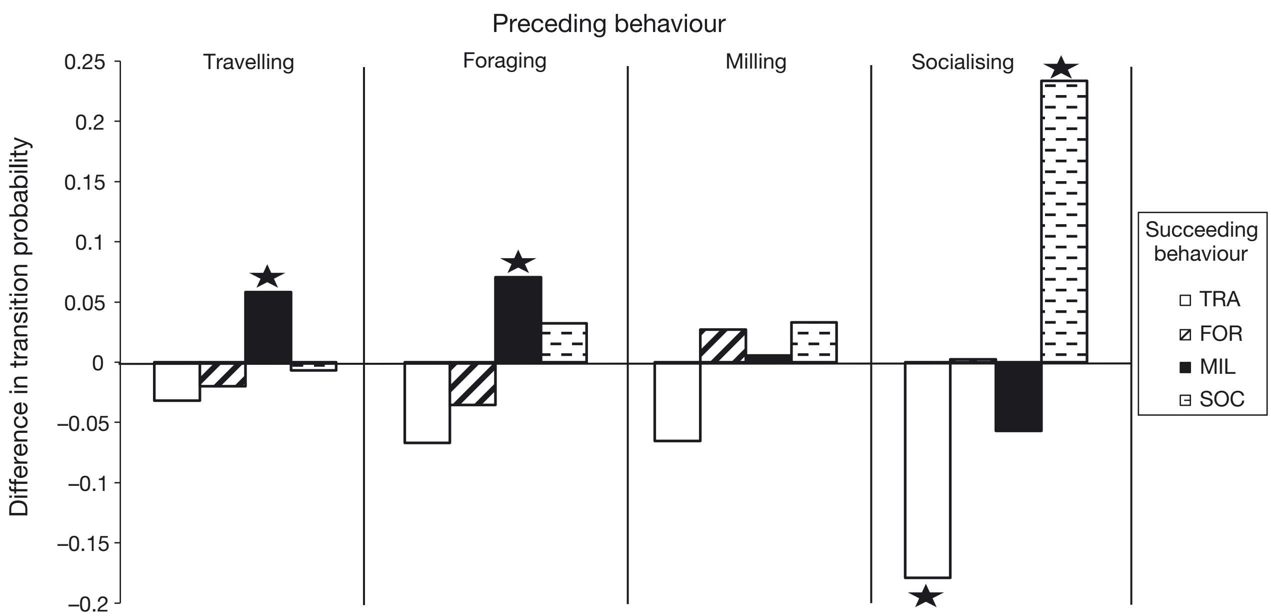

Fig. 2. Differences in transition probabilities between impact (research vessel and swim-with-dolphin vessel[s] present) and control (research vessel only) scenarios for behavioural states of Burrunan dolphins *Tursiops australis*. Vertical lines separate each preceding behavioural state, and bars represent the succeeding behavioural states (refer to legend). Transitions with a significant difference ($p < 0.05$) are denoted with a star. Behavioural states are defined in Table 1; TRA: travelling, FOR: foraging, MIL: milling, SOC: socialising

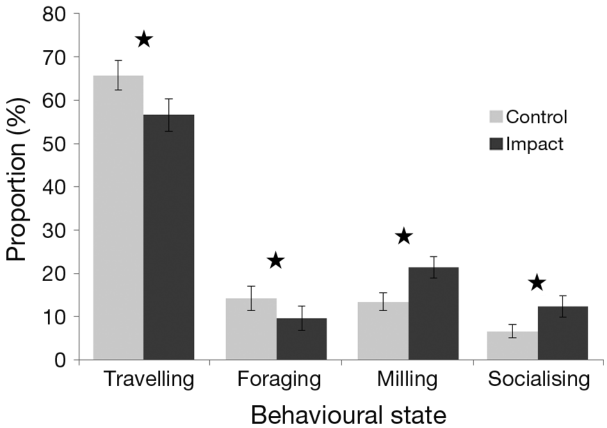

Fig. 3. Effect of swim-with-dolphin vessel interactions on the behavioural budget of Burrunan dolphins *Tursiops australis* in Port Phillip Bay, Australia. Proportion of time spent in each behavioural state during control (research vessel only present) and impact (research vessel and swim-with-dolphin vessel[s] present) scenarios. Error bars represent 95% confidence intervals. Stars indicate significant differences ($p < 0.05$). Behavioural states are defined in Table 1

($\chi^2 = 19.62$, $p < 0.001$) and socialising ($\chi^2 = 16.90$, $p < 0.001$) when in the presence of SWD vessels, to the detriment of foraging ($\chi^2 = 8.59$, $p = 0.003$) and travelling ($\chi^2 = 15.78$, $p < 0.001$).

Average bout length

Average bout length varied considerably between control and impact scenarios (Table 2). Average bout length for travelling dolphins decreased significantly by 16.3%, from 18 to 15 min (95% CI: 2.9–3.1 min; $t = 43.30$, $p < 0.001$, df = 1096) when SWD vessels were present. Bout length also decreased significantly by 13.6%, from 13 to 11 min, for foraging dolphins (95% CI: 1.5–2.1 min; $t = 10.91$, $p < 0.001$, df = 251) in the presence of SWD vessels. Furthermore, when SWD vessels were present, average bout length for socialising dolphins increased significantly by 69.4%, from 5 to 9 min (95% CI: 3.3–4.1 min; $t = 17.06$, $p < 0.001$, df = 192).

Recovery time

Foraging dolphins took longer to return to that behavioural state in the presence of SWD vessels, with the time required to return to foraging extending by 47.6%, from 21 to 31 min (Table 3). Conversely, when SWD vessels were present, there was a 46.7% reduction in the amount of time socialising dolphins took to return to that behavioural state compared to control scenarios, from 45 to 24 min (Table 3).

Table 2. Average bout length (min) of Burrunan dolphin *Tursiops australis* behavioural states during control (research vessel only present) and impact (research vessel and swim-with-dolphin vessel[s] present) scenarios in Port Phillip Bay, Australia. Behavioural states are defined in Table 1

Behavioural state	Control	SE	Impact	SE
Travelling	18.40	0.05	15.40	0.05
Foraging	13.24	0.10	11.44	0.13
Milling	6.91	0.14	7.00	0.11
Socialising	5.27	0.18	8.93	0.13

SWD vessel exposure

The yearly simulated cumulative exposure to SWD vessels varied between individuals (Fig. 4A). Throughout the year, the average proportion of time individual dolphins spent with SWD vessels each day was 5.6% (range = 5.0–6.2%) or 40 min. The estimated exposure of Burrunan dolphins to SWD vessels varied throughout the year and also between individuals (Fig. 4B), as a function of seasonal variation in the number of SWD trips.

Cumulative behavioural budgets

There was no significant effect of SWD vessels on the cumulative (i.e. yearly) behavioural budget of dolphins (goodness-of-fit test, $\chi^2 = 0.23$, df = 3, $p = 0.973$).

Table 3. Average time (min) for Burrunan dolphins *Tursiops australis* to return to a specific behavioural state in control (research vessel only present) and impact (research vessel and swim-with-dolphin vessel[s] present) scenarios in Port Phillip Bay, Australia. Arrows indicate the direction of the effect, with the upward and downward facing arrows indicating an increase and decrease in the time (min) it takes dolphins to return to a specific behavioural state between control and impact scenarios, respectively. Behavioural states are defined in Table 1

Behavioural state	Control-behavioural state resumed	Impact-control	Impact-behavioural state resumed
Travelling	4.57	↑ 0.73	5.30
Foraging	21.13	↑ 9.90	31.03
Milling	22.33	↓ 8.29	14.04
Socialising	45.09	↓ 20.85	24.24

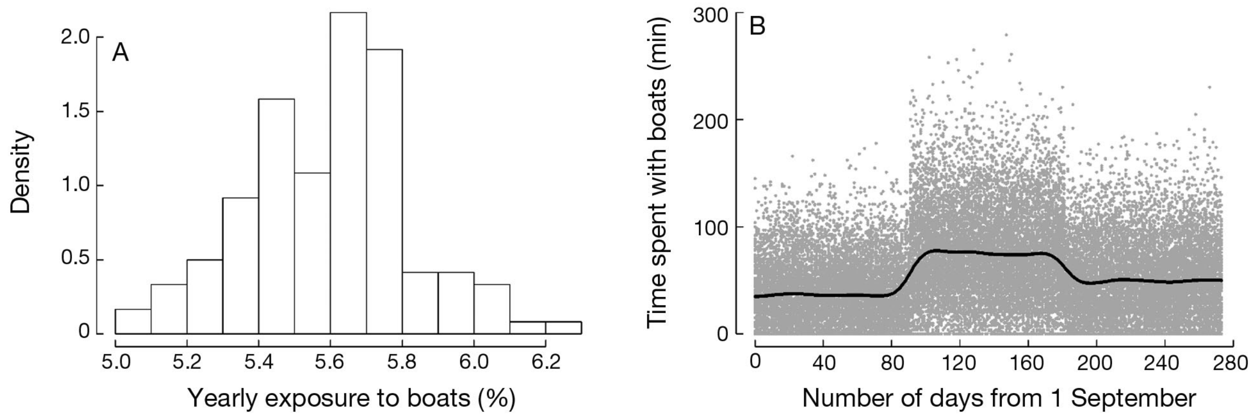

Fig. 4. (A) Yearly cumulative exposure of individual Burrunan dolphins *Tursiops australis* to swim-with-dolphin (SWD) vessels in Port Phillip Bay, Australia, measured as the percentage of time spent in the presence (<300 m) of SWD vessels. (B) Within-year variation in time spent with SWD vessels for individual dolphins throughout the year. A cubic smoothing spline (black solid line) has been fitted to the simulated data, with degrees of freedom set to 20. No SWD trips take place in winter, so those data have been omitted. The figures are based on model simulations

DISCUSSION

This study aimed to determine whether SWD vessels in PPB affect the behaviour of Burrunan dolphins. Significant short-term changes in the behaviour of Burrunan dolphins were detected as a consequence of interactions with SWD vessels. Transition analyses using Markov chains found that the presence of SWD vessels significantly affected all 4 of the behavioural states analysed. Of importance, when SWD vessels were present, the time Burrunan dolphins spent foraging was significantly reduced, with average foraging bout length decreasing, foraging recovery time increasing and the probability of transitioning from foraging to milling increasing 4-fold compared to control conditions. This decrease in time spent foraging during tourism activities could be of importance and result in a decrease in energy acquisition (Christiansen et al. 2013). Disruptions to foraging behaviour during SWD tourism interactions are likely to have greater effects on pregnant or lactating dolphins, as they have increased energetic expenses (Reddy et al. 1991, Kastelein et al. 2002). This is of concern given that Burrunan dolphin exposure to SWD vessels in PPB is greatest over the austral summer, coinciding with their peak calving season (Filby 2016).

Recent research has revealed that small groups of dolphins in PPB avoid SWD vessels significantly more frequently than larger groups (Filby et al. 2014). Given that more than half the groups encountered in PPB are small (average group size was 5 animals, Filby et al. 2017), it is unlikely that some dolphins continue to forage whilst the rest of the group interacts with SWD vessels. This may explain why foraging levels are significantly reduced in the presence of SWD vessels (Filby et al. 2017). Alternatively, specific foraging strategies within this population may result in higher susceptibility to disturbance from SWD vessels whilst foraging. Another possibility is that SWD vessels may disperse the dolphins' prey, or cause dolphins to miss prey due to engine noise (Bain et al. 2014). In both scenarios, dolphins discontinue foraging in the presence of SWD vessels and mill or socialise instead.

Using the same data, Filby et al. (2014) reported that in 39% of observations, SWD vessels illegally approached and manoeuvred through a group of dolphins. On such occasions, it is highly probable that animals within the group would become separated, their communication efficiency would be affected by the underwater engine noise, and prey, if present, would scatter (Scarpaci et al. 2000a, Williams et al. 2006, Jensen et al. 2009, Guerra et al. 2014). For each of these scenarios, it would take time for individuals within the group to re-establish contact, thus potentially explaining the significant increase in foraging recovery time for dolphins in the presence of SWD vessels that was detected in the present study, especially if dolphins were foraging cooperatively. Further, the close proximity of SWD vessels to foraging groups would likely interfere with foraging efficiency (Dans et al. 2008), which may partially explain the reduction in time spent foraging.

Regardless of why disruptions to foraging behaviours occur when SWD vessels are present, the likely consequence is a decrease in energy gain opportunities for these individuals. To reduce disruptions to foraging Burrunan dolphins, it is recommended that management should start to actively enforce compliance with regulations (i.e. issue significant fines), especially within areas highlighted as foraging hotspots (Filby et al. 2017) for Burrunan dolphins within PPB. Furthermore, it is recommended that management initiate compulsory annual training programs for owners and staff of SWD companies. This training should aim to raise awareness of all regulations pertaining to interactions with dolphins (to increase compliance levels) and how to correctly identify different dolphin behavioural states (to minimise interactions when dolphins are feeding or resting).

When SWD vessels were present, dolphins spent significantly more time milling, to the detriment of travelling and foraging. For many delphinid populations, travelling is the predominate behaviour observed in control scenarios (Hanson & Defran 1993, Neumann 2001, Jones & Sayigh 2002, Filby et al. 2013), and this is also the case for the population of dolphins in PPB (Filby et al. 2017). Previous research suggests that dolphins often engage in 'travelling' in order to locate prey (Shane 1990, Hanson & Defran 1993, Dans et al. 2008, 2012). If this is true, then dolphins in PPB that engage in increased levels of 'milling' in the presence of SWD vessels may spend less time travelling searching for prey, which could ultimately reduce the health of the population through reduced prey consumption.

The increase in milling behaviours documented in the presence of SWD vessels could increase dolphins' energy expenditure (Christiansen et al. 2014). Collectively, when combined with the reduction in time spent foraging when SWD vessels are present, this increase in milling behaviour may lead to reduced biological fitness with population level consequences (Christiansen et al. 2015), as has been documented for other populations (Bejder et al. 2006a, Lusseau et al. 2006, Williams et al. 2006, Currey et al. 2009). However, results from the cumulative behavioural budget suggest that there are no long-term effects of biological significance for this population.

Socialising behaviours increased significantly in the presence of SWD vessels. Socialising bout lengths may be longer in the presence of SWD vessels if dolphins have learnt over time to use SWD vessels as a cue to find conspecifics (Martinez 2010). This is a likely scenario in PPB given that mating behaviours were frequently observed whilst dolphins were socialising around SWD vessels. Given that socialising dolphins are 'attractive' to SWD vessels because their active surface behaviour is exciting for tourists to observe, it is likely that operators target groups that are socialising. Hence, the observed increase in socialising behaviour in the presence of SWD vessels might be a caveat from observer bias.

Although the short-term behavioural budget of the dolphin population was significantly affected, SWD vessels did not significantly affect the cumulative (i.e. yearly) behavioural budget of Burrunan dolphins, with the estimated average cumulative time that individual dolphins spent with SWD vessels each day being only 40 min. Thus, although immediate behavioural disruptions caused by SWD vessels were significant, this study reveals that it cannot always be assumed that cetacean tourism has negative effects on the targeted population (New et al. 2013, Christiansen & Lusseau 2015). Indeed, the cumulative behavioural budget results of this study suggest that the SWD tourism industry within PPB is not having long-term effects of biological significance on this small population of Burrunan dolphins, indicating that this industry may be sustainable in its present form. This conclusion would not have been reached if cumulative effects on the dolphins had not been considered. Thus, this study highlights the importance of determining cumulative exposure to vessel-induced disturbance when evaluating the effects of cetacean-swimming and/or -watching vessels on a targeted population (Christiansen & Lusseau 2015, Christiansen et al. 2015).

The individual level of exposure (5.6%) of the PPB dolphins documented here is relatively low compared to exposure levels of other delphinid populations globally, which are often exposed to repeated and prolonged interactions with tourism vessels throughout daylight hours, often during most of the year (Williams et al. 2006, Timmel et al. 2008, Christiansen et al. 2010, Mustika et al. 2013, Tyne et al. 2017). The low level of exposure observed may explain the non-significant impact on the cumulative behavioural budget of dolphins in this study. Presently, the Wildlife (Marine Mammal) Regulations (2009) limit the number of SWD permits in PPB and restrict SWD operators to approaching dolphins only 5 times per trip. The cumulative impact of the SWD tourism industry on this population being non-significant may in part be due to these regulations, as they effectively limit the time SWD vessels spend with dolphins. The Wildlife (Marine Mammal) Regulations (2009) were developed based on scientific input (Scarpaci et al. 2004).

A limitation of the present study was that transitions involving the behavioural state 'rest' had to be excluded from the analyses due to small sample size. It could be argued that because Burrunan dolphins spend such a small proportion (1.8%, Filby et al. 2017) of their time during the day resting this is not a critical component of their daytime behavioural budget. Conversely, it could be argued that because dolphins spend such limited time resting during the day, any disturbance may be detrimental. Thus, it is recommended that future research on this population obtain a larger sample size for focal follows.

Given that the population of Burrunan dolphins in PPB is small, genetically isolated and listed as 'threatened' (Victorian Flora and Fauna Guarantee Act of 1988), it is strongly recommended that management adopt a precautionary approach, capping the number of SWD and dolphin-watching permits at its current level, until such time as biologically valid data are available for resting behaviour for Burrunan dolphins in PPB. If the intensity of boat-based dolphin tourism were to increase, the cumulative exposure levels for dolphins would subsequently increase, potentially acting as a selection force for this population by influencing the fitness of individuals that use habitats where exposure to tourism vessels is higher (Milner et al. 2007). By increasing the number of permits by even 1 vessel, significant long-term impacts on a population can occur, as was discovered in Shark Bay, Western Australia, for a population of bottlenose dolphins (*Tursiops aduncus*) (Bejder et al. 2006a). By applying the precautionary principle and instigating a moratorium, management can help ensure the on-going sustainability of the dolphin tourism industry in PPB, allowing tourists the rare experience to swim with dolphins in the wild, whilst simultaneously increasing their pro-environmental beliefs and biocentric values by implementing effective on-board education (Lück 2003, Mayes et al. 2004, Stamation et al. 2007, Wiener 2013, Filby et al. 2015).

Acknowledgements. We are very grateful to Dave Lundquist (Department of Conservation) and Anna Meissner (Massey University) for providing valuable advice on Markov chain analyses. We also thank Rod Watson, the Victorian Marine Science Consortium and Sea All Dolphin Swims who were supportive of this research. Sincere thanks go to Dane Balodis for his assistance with Fig. 1. This research was generously funded through grants to N.E.F. from the Ian Potter Foundation (no. 20120026), Norman Wettenhall Foundation, ANZ Holsworth Wildlife Foundation, Massey University and by Victoria University. This project was carried out under approval of the Victoria University Animal Ethics Committee (AEETH no. 07/09), and research permits from the Department of Sustainability and Environment (Permit nos. 10005128 and 10006282).

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Editorial responsibility: Ana Cañadas, Madrid, Spain

Submitted: August 22, 2016; Accepted: March 20, 2017
Proofs received from author(s): May 19, 2017