

Whalewatching impacts on small cetaceans are most likely population specific

Leslie F. New¹, John Harwood², Len Thomas³, James S. Clark⁴, Robert Harcourt⁵ and David Lusseau⁶

¹ US Marine Mammal Commission, 43040 East-West Highway, Suite 700, Bethesda MD 20814 USA

² Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY168LB, UK

³ Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, Fife, KY16 9LZ, UK

⁴ Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

⁵ Graduate School of Environment, Macquarie University, NSW 2109, AUS

⁶ University of Aberdeen, Institute of Biological and Environmental Sciences, Aberdeen AB24 2TZ, UK

ABSTRACT:

Whalewatching is often considered to be an ecologically sound and conservation friendly way to exploit wildlife and the environment. Observation of marine mammals *in situ* can help educate the general public and can provide them with a sense of connection to the species. It has been proposed that, in turn, this may result in an increase in public support for the conservation of marine mammals and their habitat. In addition, whalewatching provides economic benefits in the form of tourism revenue. However, whalewatching also has the potential to negatively affect cetacean populations through changes in behaviour, reproductive success and movement. The species' dynamics and environment, in addition to the operators' behaviour, can determine whether whalewatching has benign or malign impacts on the population being observed. We have developed a mathematical model to describe the complex behavioural, social and spatial interactions of coastal bottlenose dolphins, *Tursiops truncatus*. We use this model to investigate the potential effects of whalewatching on a small, resident population of bottlenose dolphins in Doubtful Sound, NZ. We then investigate the potential effects of whalewatching on a larger, theoretical population with a similar response to disturbance. Our results suggest that these activities may negatively affect cetacean populations under certain circumstances. This highlights the importance of determining limitations on whalewatching approach distances, effort and activity limitations for individual populations rather than at the species or regional level.

INTRODUCTION

The potential for whalewatching activities to negatively impact the species being observed is well documented (Erbe, 2002; Hastie, *et al.* 2003; Lusseau, 2003; Lusseau & Bjeder, 2007; Williams, *et al.* 2009), and can include temporary shifts in behaviour (Lusseau, *et al.* 2009), group dynamics (Steckenreuter, *et al.* 2012), changes in habitat use (Lusseau, 2005) and shifts in vocalizations (Erbe, 2002). In addition, the intensity of a species' response to whalewatching can vary between areas (Lusseau, 2004), and may be dependent on the behaviour of the vessels, environmental conditions and the availability of resources. Given the importance of whalewatching as a non-consumptive use of the marine environment (Karczmarsky, 2000), and its profitability at local, regional and international scales (O'Connor, *et al.* 2009, Kessler & Harcourt, 2012), the potential for these activities to affect population viability in the long term needs to be assessed.

The long-term effects of whalewatching are of concern in terms of the species' conservation, but can be difficult to determine (e.g., Lusseau, 2004; Lusseau & Bjeder, 2007). As with many areas of conservation, it is the small, isolated or resident populations that are at potentially greater risk from anthropogenic activities. Large, open or migratory populations are less likely to show a permanent effect of whalewatching, since the proportion of the population impacted will be low and it is unlikely to be the same individuals interacting with the tour vessels on a regular basis. Without a way to determine the potential population consequences of whalewatching it is difficult to effectively manage the industry and conserve the species of concern.

One way to assess the consequences of a disturbance is to investigate the resulting potential changes to individual health. Health, which we define as an animal's physical condition in terms of blubber layers and general fitness, will affect survival and reproduction. The larger the proportion of a population affected, and the greater the intensity of the disturbance, the greater the probability that individual shifts in survival and reproduction will affect the population's vital rates, and thus its dynamics. However, measuring health, especially under field conditions, can be difficult. As a result, we develop a mathematical model to describe the complex behavioural, motivational, social and spatial interactions for coastal bottlenose dolphins (*Tursiops truncatus*). In this model, health is one the motivations that drives behavioural choice, since individuals in poor health will desire to take part in behaviours that will improve their condition. This model can be used to simulate the potential impacts of disturbance by accounting for the dolphins' behavioural response to vessel presence, which will then impact their motivations. Any resulting shift in the distribution of the population's health can then be used to infer potential population level effects.

We chose to model coastal bottlenose dolphins, *Tursiops truncatus*, due to their global distribution, the varying conservation status of different populations (e.g., Currey, *et al.* 2009; Fruet, *et al.* 2011) and relatively similar behavioural response to disturbance across populations (e.g., Nowacek, *et al.* 2001; Lusseau, 2006; Miller, *et al.* 2008; Steckenreuter, *et al.* 2011). Using a model developed by New, *et al.* (submitted), we explore the impact of whalewatching on a small, resident population of bottlenose dolphins in Doubtful Sound, NZ, and how this anthropogenic activity may affect the population's health, which can then be used to determine the potential long-term effects of whalewatching. We then examine the potential effects on a larger, theoretical population and compare the results.

METHODS

Dolphin schools take part in an activity (\mathbf{a}_t), that is dependent on the motivations ($\mathbf{m}_{i,t}$) of the individual dolphins within a school. We define four activities, travelling, resting, foraging and socializing, which are mutually exclusive and cumulatively inclusive. The motivational states are defined as hunger, fear, social desire and health, and are unit-less and centered at zero. Negative values indicate a lack of motivation, whereas positive values designate strong motivation. Other than health, an individual's motivation at time t is dependent on its motivation and activity in the previous time step (\mathbf{a}_{t-1}) and the season (s_t) (Hastie, *et al.* 2004) giving,

$$\mathbf{m}_{i,t} = \mathbf{m}_{i,t-1} + \mathbf{A}\mathbf{a}_{t-1} - \delta s_t, \quad (1)$$

where \mathbf{a}_{t-1} , $\mathbf{m}_{i,t}$ and δ are vectors of length k containing the activity, motivational states and the effect of season, respectively, \mathbf{A} is a k by k matrix of the cost-benefit of each activity on the motivations, \mathbf{a}_{t-1} is binary, equalling one for the activity in which the individual is engaged, but is zero otherwise, and s_t is a scalar with a value of zero for cold weather and one for warm weather.

We assume that health ($m_{c,i,t}$) is affected by an individual's hunger ($m_{h,i,t}$) rather than directly by its activity, since we would not expect to see rapid fluctuations in this metric. The relationship was determined by the assumption that individuals unmotivated by hunger have sufficient resource acquisition to maintain good health. This gives,

$$m_{c,i,t} = m_{c,i,t-1} - \beta_0 + \beta_1 m_{h,i,t}, \quad (2)$$

where β_0 ensures that when $m_{h,i,t} = 0$ there is a beneficial effect on health, and β_1 relates hunger to health.

The cost-benefit matrix \mathbf{A} is determined by dolphin biology, and the magnitude of the cost-benefit will vary with activity. In addition, since the population is not homogenous, the \mathbf{A} and β values were varied with the type of individual; mothers with calves, juveniles, and adults (adult males and non-breeding adult females).

The dolphins' activity at time t arises from the school's motivations. This is not a simple trade-off, where the most urgent need is always fulfilled (e.g., Lorenz & Kickert, 1981), but a balance between all four motivations. For computational reasons, every individual in a school is assumed to take part in the same activity. Change in the activity state is driven by the individuals' discontent or satisfaction within each motivation. The desire of an individual to take part in the different activities ($\mathbf{q}_{i,t}$) is modelled as,

$$\mathbf{q}_{i,t} = \mathbf{G}\mathbf{m}_{i,t} + \boldsymbol{\rho}s_t, \quad (3)$$

where $\mathbf{q}_{i,t}$ is a vector of length k , \mathbf{G} is a k by k matrix indicating the strength of the relationships between motivations and activities, and $\boldsymbol{\rho}$ is a vector of length k containing the effect of season on $\mathbf{q}_{i,t}$. As with the cost-benefit of activity on motivation, the matrix \mathbf{G} is determined through the species' biology. The school's desire for each activity is the mean of the individuals' desires ($\boldsymbol{\mu}_{q,t}$) and gives rise to the probability of the school taking part in each activity ($\mathbf{p}_{a,t}$) according to,

$$\mathbf{p}_{a,t} = P(\mathbf{a}_t) = \frac{\exp(\boldsymbol{\mu}_{q,t})}{\sum \exp(\boldsymbol{\mu}_{q,t})}, \quad (4)$$

where $\boldsymbol{\mu}_{q,t}$ and $\mathbf{p}_{a,t}$ are vectors of length k and $\mathbf{p}_{a,t}$ sums to one. The school's activity is then chosen according to a multinomial distribution,

$$\mathbf{a}_t \sim \text{Multinom}(\mathbf{1}, \mathbf{p}_{a,t}), \quad (5)$$

giving a vector of length k in which the chosen activity is equal to one and all other values are zero.

Dolphin populations are divided into schools whose membership is fluid (Connor, *et al.* 2000), and provides benefits in terms of decreased predation risk. Therefore, fission-fusion is assumed to depend on the size of a school and the dolphins' motivation by fear, since larger schools can provide more protection (Lusseau, *et al.* 2004). In addition to an entire school splitting, individuals can also seek to leave their current school and join another. Due to dolphins' ability to form long-lasting individual associations (Lusseau, *et al.* 2003), we assume that individual dolphins will leave their current school with their most closely associated individual. Furthermore, individuals will attempt to join a school in which they are positively associated with the group members and which is taking part in the individuals' desired activity.

Due to resource limitations in Doubtful Sound, our simulations restrict the activity of the dolphins. Schools can transition from travelling to any other activity, but cannot transition from socialising, resting or foraging to any activity except for travelling. This enables us to account for the spatial limitations imposed on the dolphins by their habitat without explicitly modelling the spatial distribution of Doubtful Sound.

When whalewatching vessels are present, the dolphins' reaction is dependent on their distance to the tour boat. An individual's fear will increase inversely with their distance to the vessel, affecting the dolphins' motivations prior to changing their activity. This allows for differences in the dolphins' observable reaction to whalewatching vessels, since schools more motivated by fear may choose to abandon their current activity more quickly than groups more driven by other motivations, such as hunger. However, if a whalewatching vessel shares the same location as a dolphin school, the group is assumed to switch their activity to travelling, in addition to increasing their motivation by fear, due to the severity of the interaction with the vessel. By modelling the dolphins' response to whalewatching vessels in this manner we are able to account for both the dolphins' visible and hidden responses to disturbance.

RESULTS

The parameter values for our simulation were determined from the biological relationship between the states of interest. For example, hunger will be increased by energetically expensive behaviours such as socialising, but will decrease when individuals successfully forage. Similarly, hungry individuals will seek to forage to alleviate this motivational need. The relative value of the cost-benefit parameters were determined through the

observation that some activities are more energetically costly than others (e.g., Yazdi, *et al.* 1999), and then scaled to avoid motivational values that inhibited computation. We explored two scenarios for the bottlenose dolphin population in Doubtful Sound, the first assuming no vessel interaction, the other assuming that each school had a time-invariant, 9% chance of encountering a whalewatching vessel each day. We chose this level of interaction based on the knowledge that the dolphins can spend as much as 9% of their day in the presence of whalewatching vessels (Lusseau, 2003). The population size was 56 individuals (Currey, *et al.* 2007) and we used a time step of one day, running the simulations for a total of 365 days with season. Season is binary, either warm or cold, and switches half way through the time steps. Although dolphins will take part in more than one activity per day, we record only a primary activity for each time step to speed computation. However, the cost-benefits of each activity are weighted according to the dolphins' motivations to account for the fact that they will have taken part in each activity multiple times throughout the course of a single 24 hour time period. We simulated each scenario 100 times to ensure the robustness of our results to the stochasticity inherent in the model, and present the cumulative outputs of these simulations for interpretation.

The activity time budgets and motivational states, particularly health, were the focus of these simulations. The predicted annual time budget of the dolphins, for both scenarios, is similar to that identified by Lusseau (2003), in both the presence and absence of whalewatching vessels, over the much shorter time scale of his study. Our simulations predict a shift in the activity budget as a result of regular interactions with whalewatching vessels, leading to a notable increase in the time spent diving (foraging in Fig. 1), since vertical avoidance was not distinguishable from that activity, as well as decreases in the time spent resting and socializing (Fig. 1).

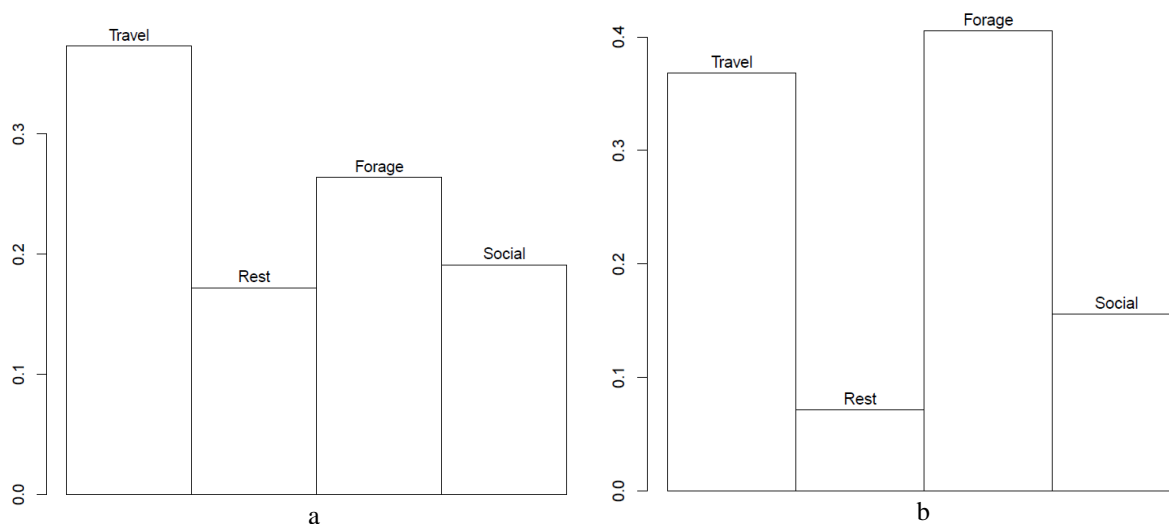


Figure 1: The activity time budgets for coastal bottlenose dolphins in Doubtful Sound in the absence (a) and regular presence (b) of whalewatching vessels.

The difficulty in obtaining information on a measure such as motivations means that data are not available to which to compare the predictions from our simulation. Therefore, we consider the relative difference between the dolphins' motivations in our two scenarios, as opposed to their absolute values. When the population is disturbed we see a notable increase in the population's motivation by hunger and fear. The population's health also declines, since the population is less satisfied with this motivation in the presence of disturbance. However, the skewness of this distribution is less pronounced than that of hunger or fear, with the mode of the distribution shifting from approximately 0.50 for an undisturbed population to 0.75 for the population exposed to whalewatching; although this is still an 50% increase in the population's dissatisfaction with health. Interestingly, there is no dramatic change in the dolphins' social desire, despite the decrease in this activity (Fig. 2).

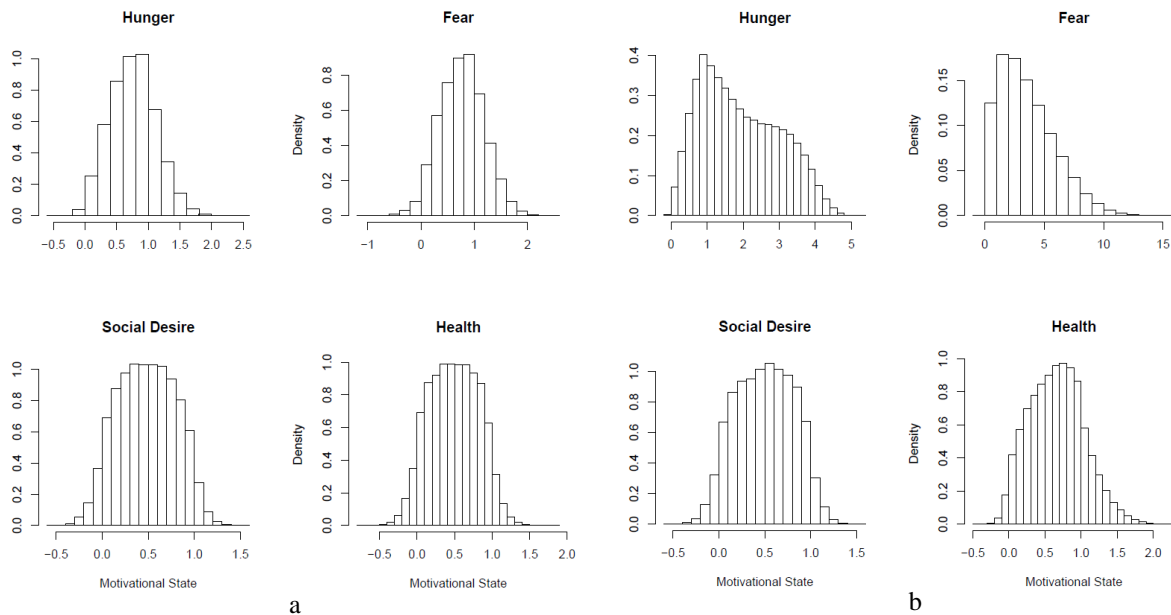


Figure 2: The distribution of motivational states for coastal bottlenose dolphins in Doubtful Sound in the absence (a) and presence (b) of whalewatching vessels.

From our simulations, we observe that a seemingly low level of disturbance can have a potentially biologically significant result when the entire population is affected. Small populations are at greater risk, since a larger proportion of the population will come into contact with each whalewatching vessel, and each individual will have greater potential value to the population. To emphasise this point, we consider a theoretical bottlenose dolphin population of 160 individuals, equal to the population size found in Sarasota Bay, Florida (sarasotadolphin.org). In this case, we will assume that the dolphins' vertical avoidance of the whalewatching vessels (Lusseau, 2003) results in a loss of 12% of their foraging time during the period in which they are interacting with whalewatching vessels, as is observed with common dolphins (*Delphinus* sp.) (Stockin, *et al.* 2008b). Since vessels can only operate during daylight, and require time to load and off-load passengers, we assume that each vessel can make a maximum of two four hour trips per day. Taking a worst case scenario, where the whalewatching vessel is able to identify and follow a single dolphin school for the entire duration of their cruise, a school would interact with the boat for 16.67% of their day. Overall, this translates into an approximately 2% decrease in total amount of time spent foraging, assuming no temporal or spatial variation in this activity or in the behaviour of whalewatching vessels. As we saw in the simulation, this level of disturbance has the potential to affect the species' activity budget and health, if the entire population is exposed to a similar level of risk.

The potential population-level effect of this intensity of disturbance will depend on the characteristics of the population. Although school size in bottlenose dolphins can vary from one individual to almost the entire population, there is a tendency towards smaller groups, so we use an average group size of eight individuals, based on the observed mode from the Doubtful Sound population (Lusseau, *et al.* 2003). Given our assumptions on vessel behaviour, it would require approximately three whalewatching vessels to impact the entire population currently found in Doubtful Sound each day. However, considering a larger population size of 160 individuals this same level of disturbance would only impact 30% of the population, or a 0.6% loss of foraging time for the population as a whole. In general, the likelihood of the entire population being exposed to a disturbance will increase with the number of whalewatching vessels, but will decrease as the population size increases.

Our estimate of the percentage of the population affected by the disturbance is almost certainly an overestimate, even when accounting for the possibility of larger school sizes, since it is unlikely that each tour boat would be able to encounter the exact same dolphins for the full four hours of operation, or that each vessel would always target separate schools. The effect of the disturbance would be further reduced for open populations, where it is unlikely that the same dolphins would be affected regularly by the whalewatching vessels. As a result, the characteristics of individual populations could render the impact of a disturbance minimal at the population-level. Unless the disturbance is a regular occurrence, a 2% reduction in foraging time on one day is unlikely to significantly impact an individual's health, given this is within the bounds of uncertainty for behavioural time budgets (Lusseau, 2003). Therefore, a population's vital rates, and thus their dynamics, will not necessarily be affected.

DISCUSSION

We looked at the potential impact of whalewatching activities on a bottlenose dolphin population in Doubtful Sound, New Zealand and on a larger, theoretical population. In both cases we make a number of strong assumptions and simplifications in order to look at the long-term effects of potentially short-term changes in behavioural time budgets. However, our results highlight the importance considering management of whalewatching activities for individual populations, as opposed to at the species or regional level.

The bottlenose dolphins in Doubtful Sound form a small, closed, resident population whose population size is equal to the school sizes of some other dolphin populations (Stockin, *et al.* 2008a). Disturbing the dolphins in Doubtful Sound results in a notable shift in the activity time budget for the population, assuming each school faces the same probability of encountering a whalewatching vessel each day (Fig. 1). This assumption is not unreasonable given the small size of the population, the restricted nature of the fjord in which they live and the intensity of whalewatching activities in the area. The time spent foraging increased in response to disturbance due to the dolphins' increased hunger, which results from the higher energy expenditure of travelling to avoid the whalewatching vessels. While our activity time budget shows an increase in time spent foraging, the population is food limited (Lusseau & Wing, 2006), so what we are observing is the extra amount of time required to match the cost associated with vessel interactions. Therefore, although there is an increase in an activity that should improve their health, the populations' health declines (Fig. 2). However, our model does not differentiate between foraging and resource acquisition, so we might expect to see a more severe decline in health than is predicted by our simulations. However, our limitations in accounting unsuccessful foraging may also help account for the lack of temporal variation in whalewatching operations, which are likely to be season dependent, and therefore slightly overestimated since we are considering a worst case scenario. We do not observe as significant a shift in health as we do in the populations' hunger, fear and behavioural time budget. This suggests that the effect on the population is less severe than the shift in behaviour may imply, although we would still expect to see an impact on the population's vital rates given that the population's dissatisfaction with their health increased by 50%. When combined with other potential anthropogenic activities, this shift in population health has the potential to significantly impact the population's growth and dynamics.

We did not do simulations to investigate the effects of disturbance on larger, potentially open, populations, but instead tried to determine the potential effects of disturbance by calculating the maximum potential lost foraging time and the percentage of population that would be targeted by whalewatching vessels. Under our assumptions, 16.67% of a dolphin's day will be spent in contact with a tour boat, during which there will be a 12% decrease in the time spent foraging. This translates into a 2% loss over the course of a 24 hour period. Using this information, we were able to determine that when the number of tour operations are limited and the population is large and open, only a small percentage of the population will come into contact with the whalewatching vessels, and no individual is likely to encounter a tour boat on a regular basis. As a result, the shift in activity time budget for such a population will not be significant, and therefore there will be no concurrent change in the species' hunger, fear or health.

The purpose behind our analyses was to uncover the potential differences between population-level responses in the face of similar disturbances. We found that, as expected, small, resident populations are at greater risk from disturbance, since a higher proportion of the population will be impacted during each disturbance event and there is no way for the population to avoid the disturbance in the long term. In contrast, for larger populations, even if they show significant changes in behaviour in response to whalewatching vessels in the short-term, there is less likely to be a population-level effect. This is due to the small proportion of the population likely to be affected by similar levels of disturbance and the low likelihood that any individual would be exposed to the disturbance on a regular basis. This is not to say that the effect of whalewatching vessels on large populations of dolphins should be discounted and ignored. If other anthropogenic activities are occurring that can impact the population, such as pollution, the addition of more minor disturbances could result in cumulative effects that have a significant negative effect on the population.

For both Doubtful Sound and our theoretical population, we assume interaction with only chartered whalewatching vessels. This ignores the potential effect of interactions with other types of sea-going craft, such as commercial vessels, fishing boats or even kayaks or canoes. To use our model in management requires more detailed inclusion of vessel types and behaviours, as well as other anthropogenic activities that may be occurring in the area. This is an on-going area of further research. However, our results to emphasize the importance of differentiating between populations when considering the management of whalewatching activities, even when the response to disturbance is similar across populations and even species. In addition, this serves to highlight the need to separate biological significance, in terms of the observed short term behavioural change, from practical significance, in terms of its effect at the population-level.

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