Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance

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Summary

1. Behavioural change in response to anthropogenic activities is often assumed to indicate a biologically significant effect on a population of concern. Disturbances can affect individual health through lost foraging time or other behaviours, which will impact vital rates and thus the population dynamics. However, individuals may be able to compensate for the observed shifts in behaviour, leaving their health and thus their vital rates and population dynamics, unchanged.

2. We developed a mathematical model simulating the complex social, spatial, behavioural and motivational interactions of coastal bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, Scotland, to assess the biological significance of increased rate of behavioural disruptions caused by vessel traffic.

3. We explored a scenario in which vessel traffic increased from 70 to 470 vessels a year in response to the construction of a proposed offshore renewables' facility. Despite the more than sixfold increase in vessel traffic, the dolphins' behavioural time budget, spatial distribution, motivations and social structure remain unchanged.

4. We found that the dolphins are able to compensate for their immediate behavioural response to disturbances by commercial vessels. If the increased commercial vessel traffic is the only escalation in anthropogenic activity, then the dolphins' response to disturbance is not biologically significant, because the dolphins' health is unaffected, leaving the vital rates and population dynamics unchanged.

5. Our results highlight that behavioural change should not automatically be correlated with biological significance when assessing the conservation and management needs of species of interest. This strengthens the argument to use population dynamics targets to manage human activities likely to disturb wildlife.

Key-words: cumulative effects, conservation, health, management, population dynamics

Introduction

There is considerable research effort to determine the biologically significant effects of anthropogenic activities on marine mammal populations (Harwood & Wilson 2001; Alter, Simmonds & Brandon 2010; Becker, Press & Allen

2011). Different studies look at the effects of disturbance on vital rates (Caswell, Fujiwara & Brault 1999; Currey *et al.* 2009b) due to their relationship to population dynamics, while others focus on the links between disturbance and behavioural change (Miksis-Olds *et al.* 2007; Tyack *et al.* 2011). Alterations in behavioural time budgets can have consequences for an individual's health through time lost foraging (Brandt *et al.* 2011), socializing or resting (Lusseau 2003b), which impacts life functions such as

survival and reproduction. Therefore, quantifying the links between anthropogenic activity, behavioural change and health can aid us in determining the biological significance of disturbance through their links to vital rates and population dynamics. In this paper, we present a framework for modelling these linkages for coastal bottlenose dolphins (*Tursiops truncatus,* Montagu) (Fig. 1) and demonstrate its utility in estimating the effects of disturbance.

Coastal bottlenose dolphins are a globally distributed species found as far north as Moray Firth, Scotland, and as far south as Dusky Sound, New Zealand. The conservation status of these populations varies, from relatively stable populations (Fruet *et al.* 2011) to those that are critically endangered (Currey, Dawson & Slooten 2009a). The populations are exposed to an assortment of anthropogenic disturbances across their range including interactions with recreational fishing gear (Powell & Wells 2011), tour boats or other vessels (Lusseau 2003b, 2006) and the construction and operation of wind turbines for renewable energy (Bailey *et al.* 2010). While the dolphins' individual behavioural response to anthropogenic disturbances appears relatively similar across populations (Nowacek, Wells & Solow 2001; Lusseau 2006; Miller, Solangi & Kuczaj 2008), the effects of disturbance on population dynamics can vary (Lusseau 2004).

For bottlenose dolphins, there is a good understanding of the linkages between disturbance and behavioural change (Nowacek, Wells & Solow 2001; Lusseau 2003a, b, 2006; Miller, Solangi & Kuczaj 2008), as well as research connecting health indicators and vital rates (Venn-Watson, Jensen & Ridgway 2011). In addition, the links between vital rates and population dynamics are well understood (e.g. Caswell 2001) and have been investigated for this species (Currey *et al.* 2009b). However, little is known about the connections between behavioural change and individual health. This is an important gap in our knowledge, because statistically significant changes in behaviour will not impact vital rates if individuals are able to compensate for these interruptions, leaving their health relatively unaffected. In this case, the species' population dynamics would remain unaffected. Therefore, the ability to quantify the links between disturbance, behavioural change and health can help to differentiate between biological and statistical significance when trying to mitigate the effects of disturbance on the conservation status of wildlife populations. Here, we develop a mathematical

framework to simulate the complex social, spatial and behavioural interactions of coastal bottlenose dolphins in the Moray Firth, Scotland. The model is then used to investigate the effects of proposed increases in vessel traffic in the area.

Materials and Methods

BEHAVIOUR, ACTIVITY AND MOTIVATIONS

We consider the recorded behaviour of dolphin schools (column vector $\mathbf{b}_t$) at time t to be an observation, with error, on a true underlying activity (column vector $\mathbf{a}_t$) of the school. Activities are dependent on the individual dolphins' motivations (column vector $\mathbf{m}_{i,t}$) for the individual dolphins i at time t, which are driven by the cost-benefits of their current activity (Fig. 2). We defined the activity budget of the population as being composed of four main activities (travelling, foraging, socializing and resting). The activities in which the dolphins can take part are the same as the behaviours: travelling, resting, foraging and socializing. All activities and behaviours are mutually exclusive. The motivational states are defined as hunger, fear, social desire and health, where health is the animal's physical condition in terms of blubber layers and physical fitness. While health can provide context for the other states, poor health will also drive individuals to make decisions to improve their condition, thus its inclusion as a motivation. The choice of motivational states arose from the perceived primary drivers behind the observed behaviours; foraging occurs due to hunger, fear leads to a flight response (i.e. travelling), the desire to interact with conspecifics (i.e. social desire) results in socializing (e.g. play, mating) and health effects resting, while also determining adult survival and reproductive capabilities.

The motivational states are real valued, unit-less measurements centred at zero, where negative values indicate a lack of motivation (i.e. 'satisfaction') and positive values indicate strong motivation (i.e. 'discontent'). With the exception of health, an (*i*th) individual's motivation at time t ($\mathbf{m}_{i,t}$) is dependent on $\mathbf{m}_{i,t-1}$ and its activity in the previous time step ($\mathbf{a}_{t-1}$). Bottlenose dolphin activity time budgets shift with the season (constant s_t) (Grellier & Wilson 2003; Hastie *et al.* 2004; Miller, Solangi & Kuczaj 2010), so their motivations must also be affected by season, because they drive activity choice. Therefore, we have,

$$\mathbf{m}_{i,t} = \mathbf{m}_{i,t-1} + \mathbf{A}\mathbf{a}_{t-1} - \delta\mathbf{s_t}, \qquad \text{eqn 1}$$

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 warmer weather decreases the need to forage, due to
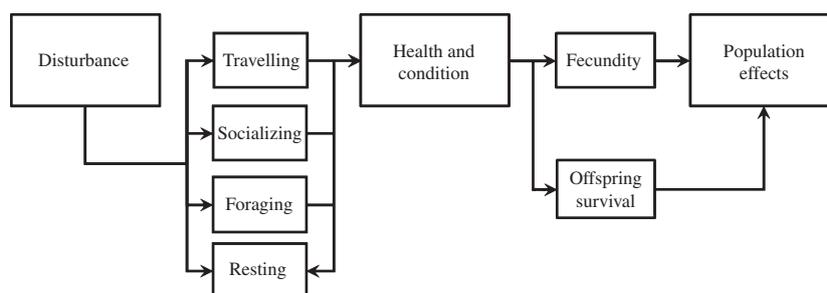
Fig. 1. A flow chart illustrating how disturbances resulting in individual behaviour change could affect bottlenose dolphin population dynamics through changes in fecundity and offspring survival.
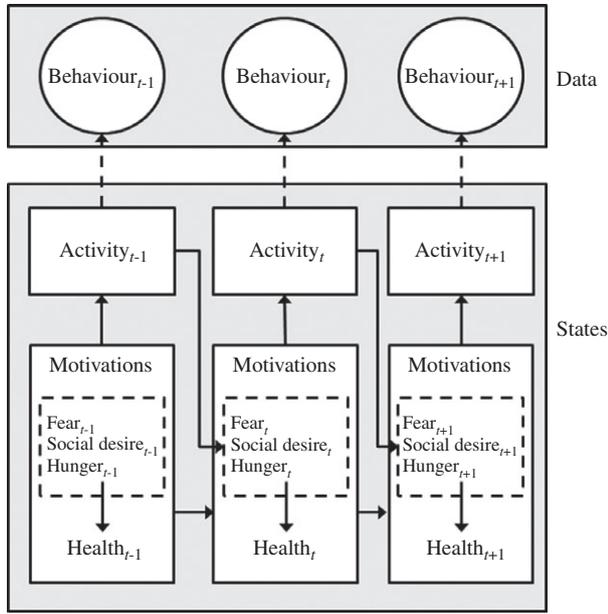
Fig. 2. A graphical representation of the model describing the change in dolphin motivation and behaviour through time. The states (square boxes) change according to the process model (solid arrows), while the data (circles) arise according to the observation model (dashed arrows).

Table 1. How each activity (rows) may increase (+), decrease (−) or fail to affect (0) an individual's motivation (columns). Health is affected indirectly by activity through an individual's hunger, which is why the values for that column are all zero

	Hunger	Fear	Social Desire	Health
Travelling	+	−	0	0
Foraging	−	+	0	0
Resting	+	−	+	0
Socializing	+	+	−	0

higher food availability and less need for insulating blubber layers (Meagher *et al.* 2008).

An individual's health ($m_{c,i,t}$, a scalar component of the vector $\mathbf{m}_{i,t}$ where c is used to indicate health) is a composite measure of its ability to survive and reproduce. From a biological standpoint, there should not be constant, wide fluctuations in this motivation. Yet, this would occur if health was directly dependent on the individual's activities. Thus, we assume that health is affected by an individual's hunger ($m_{h,i,t}$, a scalar component of the vector $\mathbf{m}_{i,t}$ where h is used to indicate hunger) and is therefore only indirectly impacted by activity. As a result, health will change at a slower rate than the other motivations. Our choice to model health as being dependent on hunger arises from the fact that when an individual is not driven by hunger, satiation is implied, so the individual will be able to maintain good health. This gives,

$$\mathbf{m}_{c,i,t} = \mathbf{m}_{c,i,t-1} - \beta_0 + \beta_1 \mathbf{m}_{h,i,t}, \qquad \text{eqn 2}$$

where β_0 ensures that when $m_{h,i,t} = 0$, there is a beneficial effect on health because 'satisfaction' is indicated by negative values for the motivation states and β_1 relates hunger to health. Health provides important context for activity choice that cannot be had from hunger alone. For example, individuals in poor health may wish to continue foraging despite high levels of fear, whereas individuals in good health in the same situation would seek to travel.

The cost-benefit of each activity is based in the species' biology. Hunger is assumed to decrease with foraging, but increase with travelling, socializing and resting due to energy expenditure. In contrast, fear increases with foraging and socializing, because these may increase the risk of predation or encountering unfavourable situations, but decreases with travelling and resting, which allow the dolphins to flee an area or remain in a safe haven. Finally, social desire is decreased by socializing and increased by resting, which may prepare the dolphins for higher levels of activ-

ity (Table 1). The magnitude of the cost-benefit will vary with activity; for example, hunger is increased more quickly by socializing then travelling, because more energy is expended in social displays than by swimming at a steady pace (Yazdi, Kilian & Culik 1999). In addition, because the population is not homogenous, the **A** and β values were varied with the type of individual: mothers with calves, juveniles and adults (adult males and nonbreeding adult females).

The dolphins' activity at time t is dependent on their motivations. For example, a school strongly motivated by hunger would be likely to forage, while one motivated by fear would be more likely to travel (flee). However, it is not a simple trade-off, where the most urgent need is the one fulfilled (e.g. Lorenz & Kickert 1981). Instead, motivations need to be balanced simultaneously to give rise to a single activity at each time point. We assume that all individuals in a school take part in the same activity and that if a school's needs are being met, it will not seek to change activity. However, as the individuals forming the school become increasingly discontent or satisfied, they will drive the school to change from one activity state to another. We can model an individual's desire to take part in the different activities (column vector $\mathbf{q}_{i,t}$) as,

$$\mathbf{q}_{i,t} = \mathbf{Gm}_{i,t} + \rho s_t, \qquad \text{eqn 3}$$

where $\mathbf{q}_{i,t}$ is a vector of length k, **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 effect of motivation on activity is determined through the species' biology. The desire to forage is positively associated with hunger because the only way to reduce hunger is to capture prey. Healthy individuals are more likely to be having their needs met, so the desire to rest is positively associated with health. The desire to rest is also negatively associated with fear, because a frightened animal is unlikely to stay in an area in which they feel unsafe (Heithaus & Dill 2002). Social desire is positively associated with the desire to socialize, which is also affected by the season (Miller, Solangi & Kuczaj 2010). Finally, the desire to travel is positively associated with fear, but inversely related to hunger. The latter occurs because travelling can be equated with a flight response, which may be suppressed by individuals that are highly motivated by hunger, since the need for energy intake would outweigh the possibility of predation (Table 2) (Heithaus & Dill 2002). Furthermore, when schools make the decision to forage, they may already be in a location in which this activity can take place, negating the need to travel and forcing a false dependency if hunger always drives the need to forage. The school's desire for each activity is based on the mean of the individuals' desires ($\boldsymbol{\mu}_{q,t}$, a column vector with length equal to the number of motivational states) and is used to obtain the probability of the school taking part in each activity ($\mathbf{p}_{a,t}$):

Table 2. How the desire for each activity (rows) is positively associated (+), negatively associated (−) or unassociated (0) with an individual's motivation (columns)

	Hunger	Fear	Social Desire	Health
Travelling	−	+	0	0
Foraging	+	0	0	0
Resting	0	−	0	+
Socializing	0	0	+	0

$$\mathbf{p}_{a,t} = P(\mathbf{a_t}) = \frac{\exp(\mu_{\mathbf{q,t}})}{\sum \exp(\mu_{\mathbf{q,t}})}, \qquad \text{eqn 4}$$

where $\mu_{q,t}$ 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:

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

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

The probability of successfully observing the true underlying activity of the school is reliant on the probability of misidentification, which can be dependent on the activity if certain activities are more likely to be confused than others, or equal for all activities. This gives the probability of observing each behaviour at time t ($\mathbf{p}_{b,t}$) as:

$$\mathbf{p}_{b,t} = P(\mathbf{b}_t) = \mathbf{P}\mathbf{a}_t, \qquad \text{eqn 6}$$

where $\mathbf{P}$ is a k by k matrix of the probability of misidentification and $\mathbf{p}_{b,t}$ is a vector of length k and sums to one. Therefore, the observed behaviour at time t is

$$\mathbf{b}_t \sim \text{Multinom}(1, \mathbf{p}_{b,t}), \qquad \text{eqn 7}$$

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

MOVEMENT

Bottlenose dolphin activities are spatially explicit (Hastie *et al.* 2004). For example, while schools can travel through any area of their habitat, only some areas are suitable for foraging due to prey availability. Therefore, we model the location and movement of schools within a population. In our model, schools move according to a directed random walk (e.g. Schmidt, Knowles & Simmons 2011), choosing a new location according to a probability based on the suitability of neighbouring locations for the group's desired activity (e.g. foraging), as well as their proximity. This accounts for the potential role of leaders within the school directing other members to desired resources (Lewis, Wartzok & Heithaus 2011).

Dolphins are rarely completely stationary, and we assume they travel small distances even when foraging, resting or socializing. Should a school's desired activity not be possible in their current location, our model requires the school to travel to an area in which the activity can take place, retaining the memory of the desired activity throughout the transit period. Only upon reaching a suitable location, will the school take part in the desired activity, and a change in activity cannot occur prior to that point. Therefore, there are situations in which schools will travel in search of prey. However, in these cases, travel occurs to meet the motivation to feed, as opposed to an inherent choice to travel, so fear remains the primary driver of the desire to travel, even though it is not the only reason to engage in this activity.

SOCIAL STRUCTURE

Dolphins live in schools of which membership is fluid; the school composition changing at various rates (Connor *et al.* 2000; Lusseau *et al.* 2006). School size varies and is typically 5–9 in the Moray Firth (Lusseau *et al.* 2004). School membership confers benefits to individuals including increased prey detection rate and decreased predation risk. The rate at which individuals interact can influence their behaviour (Lusseau & Conradt 2009).

We assume fission–fusion at the school level to be dependent upon school size and fear, because larger schools can provide more protection from predation up to a threshold (Acevedo-Gutiérrez 2002). Smaller schools are more likely to fuse, and the probability of fusion will increase linearly with rising levels of fear, because there is safety in numbers. However, once the school grows beyond an optimal size, the probability of fission will increase because individuals will face growing competition for resources and decreasing safety benefits (Lusseau *et al.* 2004). While our model allows fission to take place at any time, fusion is constrained to occur only when schools are within a 5 km radius of one another.

In addition to fission–fusion at the school level, individuals may choose to leave their school and join, or form, another. Within our model, individual dolphins must balance their personal desire (e.g. to forage) against the safety of being in a school whose activity (e.g. travelling) is contradictory. If at time t and $t-1$, an individual is completely discontented with any motivation or fully satisfied with regard to hunger, fear and social desires, then it may consider changing schools to fulfil its needs. Satisfaction with health is not included, because we assume an individual would not leave a school in which it was maintaining good health if all its other needs are being met.

If the criteria to change schools are met, the dolphin will do so with a probability dependent on fear and current school size. A new school is chosen based on its proximity, activity and average association with the proposed new school, which is determined by the type of individual (Lusseau & Newman 2004). We assume that individuals in the same class show higher associations, while juveniles and mothers with calves are negatively associated to allow for juvenile dispersal (e.g. McHugh *et al.* 2011a), and adults are neutrally associated with the other two classes. In the simulations, the values for the association matrix are assigned randomly within these constraints. Because dolphins can form long-lasting individual associations in this population (Lusseau *et al.* 2006), we assume that when a dolphin leaves its current school, it will do so with its most closely associated individual. If the individuals leave their current school, but no suitable existing school is within travelling distance, a new school of two individuals will form. Single individuals left without a school will join the closest existing school, assuming that the benefits of being in a school outweigh being alone no matter the cost of reaching the new location (Lusseau *et al.* 2004). This includes rejoining the same school the individual just left. The simulations are robust to these assumptions, as evidenced the lack of sensitivity in the model results when simulations were run with different, or relaxed, assumptions of association.

Although the model, as presented, requires that all individuals in the school take part in the same activity, we also investigated the assumption that individuals within the school take part in separate activities under constraints imposed by the school's location (Appendix S1). The resulting activity budget and distribution of motivations differed between the two assumptions (Fig. 3 and Fig. A1 [in Appendix S1]), but both produce biologically realistic dolphin populations. Therefore, the decision to model activities at the school level was based solely upon practical considerations, as opposed to biological theory, because the school model required less computational time. Furthermore, data on dolphin activities are often collected at the school level (e.g. Lusseau 2003b), and we wished our simulation to be able to reproduce the type of data that would typically be available to researchers and decision makers.
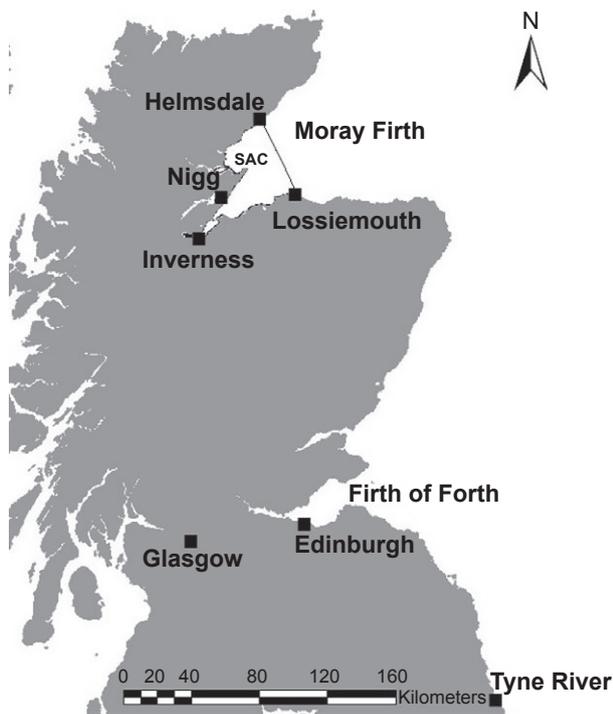
MORAY FIRTH, SCOTLAND

Bottlenose dolphins can be found in the Moray Firth year-round, forming the only known resident population in the North Sea, although individually identified dolphins have been found as far south as the Firth of Forth (Wilson, Thompson & Hammond 1997), and on one occasion near the Tyne river mouth (Thompson *et al.* 2011) (Fig. 4). These dolphins are highly coastal, rarely being observed in offshore areas (Cheney *et al.* 2012). The population size has been recently estimated at 195 (95% HPDI 162–253) dolphins (Cheney *et al.* 2012). This is a relatively small population and, when combined with their isolation, may make the dolphins
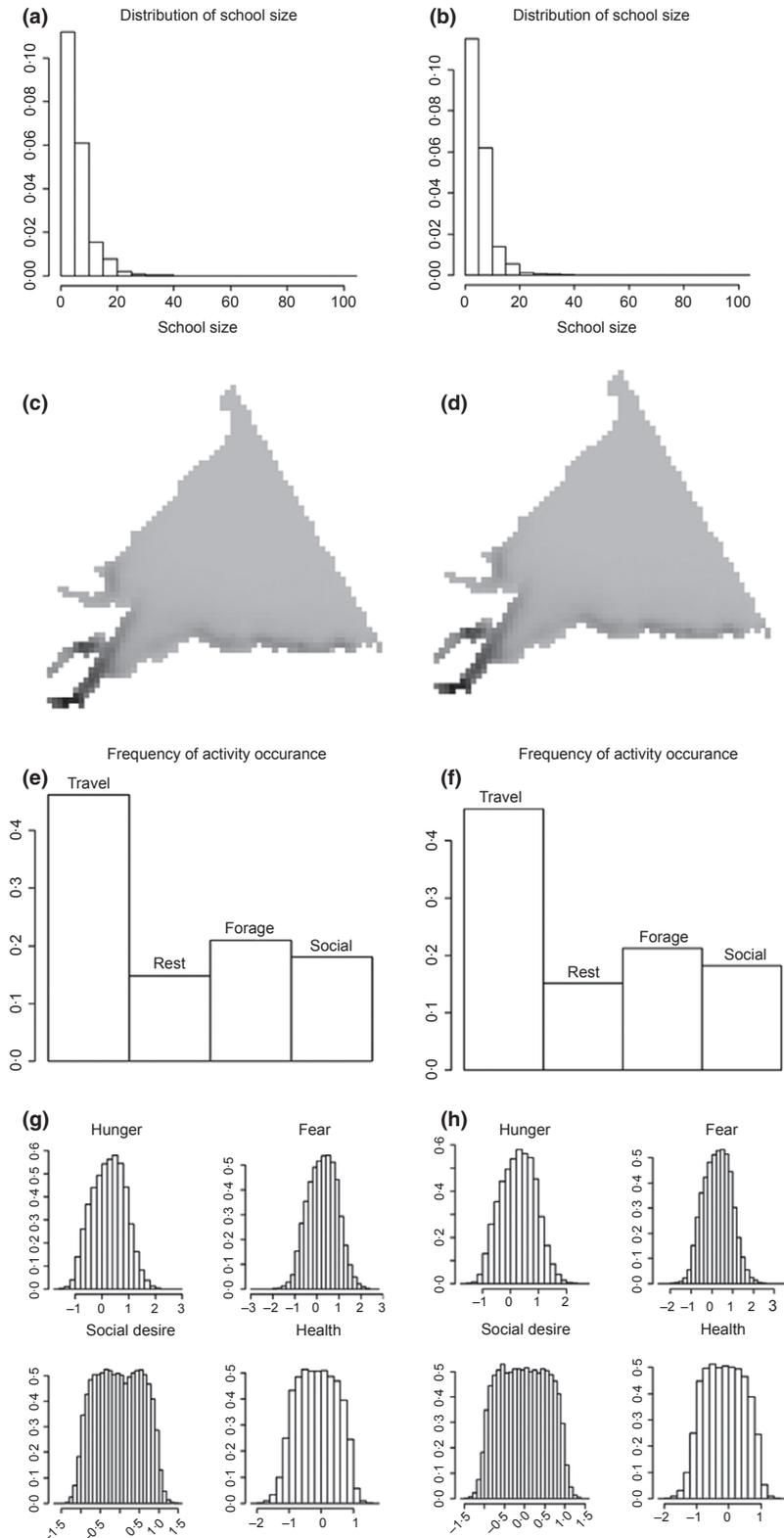
Fig. 3. Metrics for comparing the coastal bottlenose dolphin population in the Moray Firth at current (left column) and increased (right column) levels of vessel traffic. This distribution of school sizes is relatively unchanged from the status quo (a) to the disturbance scenario (b). The frequency of use for each location is similarly unchanged from current levels (b) to increased vessel traffic (d), where darker colour equals higher density of dolphin schools. The dolphin's activity budget when faced with increased disturbance (f) is similar to that observed under the current levels of boat traffic (e). Only the dolphins' motivations show a change from current to increased levels of vessel traffic (g and h, respectively), with schools being more motivated by fear.

Fig. 4. A map of Scotland identifying key features, including the Moray Firth, Nigg and the Special Area of Conservation (SAC)

more susceptible to disturbance (Thompson *et al.* 2000). As a result, the Moray Firth was designated a Special Area of Conservation under the EU Habitats Directive (92/43/EEC) to protect the population (Thompson *et al.* 2000; Bailey *et al.* 2010).

In addition to its relevance for conservation, the Firth is economically important, including activities such as dolphin watching, oil extraction, military training, commercial fishing, transportation, recreation and wind farms (Harding-Hill 1993; Bailey *et al.* 2010). Given that bottlenose dolphins change their behaviour in response to disturbance (Lusseau 2003a), the economic activities in the Firth could potentially have negative impacts on the dolphin population (Bailey *et al.* 2010).

Our model was made specific for the Moray Firth by defining locations within the Firth on a 1 km^2 grid map and calculating the geodesic distance between each water-based cell. Suitable locations for feeding were identified based upon the bathymetry (Hastie *et al.* 2004), as well as the combination of rapid change in bottom relief with strong tidal currents (Wilson, Thompson & Hammond 1997) (Fig. 5). The time step was considered to be a day, and each simulation was run for the time period of a year, with a change in season at the halfway point. In reality, dolphin activity and location change several times a day, but we simulate a single measurement for each time step that can be considered a daily average of these metrics. The costs and benefits are therefore weighted by the schools' motivations to account for the other activities that would occur within the 24 h time frame. Although the dolphins' risk of predation in the Moray Firth is low, it is not nonexistent. Orcas have been sighted in the Firth, and intraspecific aggression does occur, which can lead to infanticide (Patterson *et al.* 1998), so fear of predation and other unfavourable situations remains an appropriate driver of the dolphins' behaviour.

DISTURBANCE

We are interested in simulating the dolphins' response to disturbance under a scenario addressing economic development within the Moray Firth. In this case, disturbance will take the form of
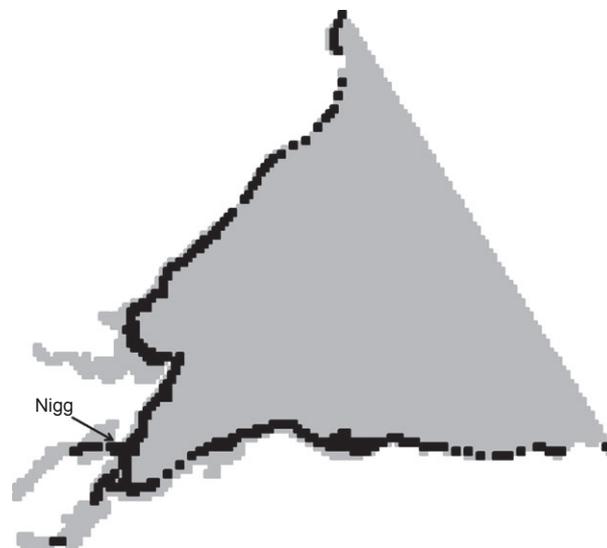
Fig. 5. The 1 km^2 grid map used to define dolphin movement and location in the Moray Firth, Scotland. Feeding areas, based on bathymetry, are in black. The location of Nigg, which is the site of the proposed renewable facility, has also been identified.

vessel traffic moving through the Firth from the local ports. For each cell, the average number of vessel hours each day of the year was estimated from available boat data (Lusseau *et al.* 2011). This was then translated into the probability that a school of dolphins would encounter a boat at each time step.

Bottlenose dolphins' observed response to vessel approaches increases with the vessel's proximity (Nowacek, Wells & Solow 2001). Therefore, if a school detects the presence of a boat, we assume that fear increases inversely with the distance from the vessel. With continued disturbance, the dolphins' fear will outweigh their other motivations and the school will decide to travel. However, if the boat shares the same location as the school, we assume that not only does fear increase, but the school will automatically switch its activity to travelling. Except when under immediate 'threat,' the reaction of dolphins to a disturbance will be dependent on all their motivations, not just fear. For example, schools that are experiencing extreme hunger may be less likely to stop foraging, because this motivation may outweigh their fear and thus their desire to travel. For our disturbance scenario, we considered a situation in which there was an increase in the number of boats at Nigg in the Cromarty Firth (which is part of the Moray Firth, Fig. 5), from 70 to 470 vessels, to investigate the potential effect of a new offshore renewable fabrication facility in the area. The speculated increase in commercial traffic was assumed to behave in a very similar fashion to existing commercial sailings to this port. Specifically, the AIS (automatic identification system) provided historic vessel tracks and the simulated increases moved similarly in region, subject to some stochasticity. Notably, these commercial vessel movements to Nigg (historic and speculative) form a generally small proportion of the vessel traffic in the Moray Firth in terms of vessel hours per 1 km^2 cell. This type of disturbance differs from other vessel disturbance studies because these vessels do not target dolphins for viewing but are only passing by the animals. The species responds differently to targeting traffic such as tour or recreational dolphin-watching boats (Mattson, Thomas & St. Aubin 2005). The dolphins are assumed to be habituated to all existing vessel traffic in the Firth. This is a reasonable assumption, given that the baseline data for dolphin use of the Firth have all been collected in the presence of the existing vessel traffic (e.g. Wilson, Thompson & Hammond 1997; Hastie *et al.* 2004).

Results

Using a population of 195 dolphins, we ran 100 simulations for the disturbance (470 vessels) and the status quo (70 vessels) scenarios and based our results on the cumulative outputs from each. For current levels of vessel traffic, school sizes ranged from two to almost 50 individuals, with a tendency towards smaller sizes (Fig. 3a). The simulated distribution of dolphin locations within the Firth (Fig. 3c) closely resembles what has been observed (Bailey & Thompson 2009), with the highest concentrations around Kessock and the Inverness and Cromarty Firths. This is interesting as we had limited constraints on the movement of dolphins; although feeding was limited by bathymetry and tidal features (Fig. 5), the dolphins' distribution was not even across all possible feeding areas (Fig. 3c,d). The average activity time budget of the dolphins is also biologically realistic, showing similar patterns to what is observed in other populations (Hanson & Defran 1993; Lusseau 2003b; McHugh *et al.* 2011b) (Fig. 3e). The distributions for the schools' motivations are all symmetric, with schools tending to be slightly more motivated by fear and hunger than by health (Fig. 3g). The model results showed no practical sensitivity to our assumptions regarding the social structure of the bottlenose dolphin population.

In our disturbance scenario, increased vessel traffic was limited to movement in and out of Nigg, in the Cromarty Firth (Figs 4 and 5). The limited spatial impact and the large area available to the dolphins (Fig. 3d) meant that we did not observe a noticeable change in dolphin group size, spatial distribution or activity budget due to the increased number of vessel hours per km^2 (Fig. 3b,d,f, respectively). Despite the large increase in the potential for disturbance, schools could avoid contact with the vessels and retreat to 'undisturbed' areas.

Discussion

We have successfully constructed a mathematical framework that describes the complex behavioural, motivational and social structure of bottlenose dolphins. Through comparison with observed data, we can determine that the model accurately simulates the behavioural time budget, spatial distribution and school size distribution observed in the Firth under current levels of vessel traffic (Fig. 3a,c, e). The tendency towards smaller schools is likely to be a result of the spatial limitations on fusion, but is consistent with the observation of smaller schools in inshore populations (Wells, Boness & Rathburn 1999). Differences between the survey-based (Wilson, Thompson & Hammond 1997; Hastie *et al.* 2004; Thompson *et al.* 2011) and simulated spatial distribution of dolphins can be accounted for by the simplification of the effects of oceanographic features on dolphin foraging in our model. While we use bathymetry and tidal currents to determine foraging areas, other features, such as the coastal topography, may also

help determine where dolphins feed. Furthermore, our simulations record a single location for each day, so we do not track the dolphin's full use of space.

The motivational distributions (Fig. 3g) also appear reasonable, although there is currently no way to ground truth our estimates. The slightly higher motivation by fear would result from the maintenance of good health, which requires foraging, which increases fear. The relatively symmetrical shape of the distributions indicates a population capable of meeting its needs, because it is not being driven by any single motivation. Strongly skewed distributions would imply that the population's needs are not being met because extreme satisfaction with one motivation (e.g. hunger) can only occur at the cost of extreme discontent with another (e.g. fear).

The results from the disturbance scenario indicate that there was no real affect of the increased vessel traffic (Fig. 3b,d,f,h). Any reaction to the disturbance would first appear in the dolphins' motivations. Therefore, the consequences of the disturbance would not necessarily be evident from standard, directly observable metrics. This implies that there may be a hidden cost of disturbance not currently being accounted for in management and conservation plans designed to determine a population's response to anthropogenic activities. This unobservable change in motivation may be what drives the shift from short-term vertical or horizontal avoidance of boats to long-term strategies involving a shift in the population's spatial distribution (Lusseau 2004; Bejder *et al.* 2006).

With minor modifications to account for different geographic features and time-scales, the model framework presented here is capable of mimicking the observed dynamics of dolphin populations outside the Moray Firth. This can allow us to explore the importance of regional factors in determining population growth and structure. Furthermore, adapting the model to account for survival and reproduction would enable us to extend the time frame of the simulation beyond a year, facilitating our ability to investigate the cumulative effects of disturbance on bottlenose dolphin populations. In its current form, the model allows us to estimate the effects of disturbance within a year and establish whether changes in behaviour in response to disturbance are biologically significant.

Determining the effect of disturbance on health is an important step in estimating potential changes in population viability, because short-term changes in behaviour need not be correlated with biologically significant effects on population dynamics. Indeed, our simulations found only a small increase in the dolphins' fear and hunger in response to disturbance, but no change in health. Although there were alterations in the dolphins' immediate behaviour in response to disturbance, the lack of change in the overall activity time budget and motivations implies that the dolphins were able to compensate for time lost in activities due to disturbance. Given that there was no real change in health between the scenarios, the population's vital rates are unlikely to be affected,

and thus, the population dynamics will remain unchanged. Therefore, our model implies that if the construction of the offshore renewable facility at Nigg is the only source of increased anthropogenic activity within the Moray Firth, then the disturbance will have a minimal effect on the viability of the bottlenose dolphin population over the course of a year. As a result, small-scale changes in behaviour should not be automatically associated with a need to cease or mitigate anthropogenic activities without further investigation as to the cumulative effects of the disturbance.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Electronic Supplementary Material: Model for Individual Activity