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Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences

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Human activities that impact wildlife do not necessarily remove individuals from populations. They may also change individual behaviour in ways that have sublethal effects. This has driven interest in developing analytical tools that predict the population consequences of short-term behavioural responses. In this study, we incorporate empirical information on the ecology of a population of bottlenose dolphins into an individual-based model that predicts how individuals' behavioural dynamics arise from their underlying motivational states, as well as their interaction with boat traffic and dredging activities. We simulate the potential effects of proposed coastal developments on this population and predict that the operational phase may affect animals' motivational states. For such results to be relevant for management, the effects on individuals' vital rates also need to be quantified. We investigate whether the relationship between an individual's exposure and the survival of its calves can be directly estimated using a Bayesian multi-stage model for calf survival. The results suggest that any effect on calf survival is probably small and that a significant relationship could only be detected in large, closely studied populations. Our work can be used to guide management decisions, accelerate the consenting process for coastal and offshore developments and design targeted monitoring.

1. Introduction

Management decisions regarding the effects of human activities on wildlife should ideally be taken before targeted populations start declining. However, it is hard to predict the long-term consequences of anthropogenic impacts [1], especially for long-lived marine predators [2]. As a result, it might be too late to act effectively by the time a negative trend in population size is detected [3].

There are modelling tools to assess the viability of populations following the direct removal of individuals [4]. However, human activities do not necessarily kill or injure exposed animals. They may, instead, sublethally disturb their activity patterns [5–7]. Recent research has focused on how changes in behaviour alter the dynamics of populations, with the aim of developing a framework to predict the population consequences of disturbance before conservation status is compromised [8,9]. This requires a mechanistic understanding of the relationship between changes in an animal's activity and its vital rates, such as survival probability and reproductive success [10–12]. This relationship can be disrupted if disturbed individuals are unable to maintain their energy

balance and lose condition [8,13]. Behaviourally mediated cascades that lead to long-term effects on population dynamics have been documented in response to changes in predation risk [14]. There is a growing body of evidence showing that animals perceive human disturbance as a form of predation risk [15,16], implying that responses to disturbance may invoke similar cascades.

Any behavioural response to disturbance will depend on an individual's internal state, its perceived risks and habitat quality [17,18]. Previous work has shown that behavioural temporal dynamics can be modelled successfully through the integration of an individual's motivational states, which combine the effects of external stimuli and physiological needs [19–21]. Because motivations are unobservable, mechanistic models are required, and agent- or individual-based models have been used for this purpose [22,23]. Predicted changes in an animal's internal states can then be linked to its energy balance and condition to understand how its allocation of energy to survival or reproduction will be impacted [8,10]. However, information on individual condition is rarely available for wild animals. Previous work has attempted to link changes in behaviour directly to fitness [11,12], but the success of this approach depends on the sample size available to inform the models as well as on the severity of the disturbance effects [24]. Detecting such a relationship may prove difficult if individual heterogeneity is large and the effect size is small, but the precise sampling requirements for a robust assessment are unclear.

While anthropogenic activities have repeatedly been shown to affect the behaviour of marine mammals at sea [7,25], few studies have attempted to link changes in behaviour to an individual's vital rates [8,22]. However, it is possible to quantify behavioural changes, individual exposure rates, undisturbed patterns of activity, and survival and reproductive success for some coastal populations of pinnipeds and cetaceans. For example, the small population of approximately 195 (95% density interval: 162–253) bottlenose dolphins *Tursiops truncatus* (hereafter 'dolphins' or 'bottlenose dolphins') that range along the East coast of Scotland has been the subject of long-term research [26,27], and information is available on their distribution and habitat preferences [28,29], as well as the reproductive history of individual animals [30]. Dolphins distribute close to the coast, with marked individual differences in habitat use [28], and appear to forage in discrete patches in their habitat associated with specific bathymetric and tidal features [29]. Some individuals consistently use areas within the inner Moray Firth [31], which has been designated as a special area of conservation (SAC) for the species under the European Habitats Directive (92/43/EEC). Marine industrial developments have been proposed in this area because of its strategic importance for traditional and renewable energy exploitation in the North Sea. These will involve increased boat traffic and coastal development (e.g. construction or enlargement of harbours, with associated piling, dredging and dumping activities), which could compromise the population's 'favourable conservation status' (a regulatory target that the UK must maintain under European legislation). Such uncertainty can lengthen the time it takes to reach a consenting decision for these developments. These uncertainties can be reduced using modelling approaches that provide robust and easy to communicate predictions of possible long-term effects. Previous work has developed a theoretical framework to model the consequences of human disturbance on individual animals [22], but such tools need to have a strong empirical grounding in order to provide robust management advice.

The aim of this study is to construct a predictive tool for assessing the risks to the conservation status of a dolphin population posed by new developments. First, we develop an individual-based model for bottlenose dolphin behavioural dynamics in the Moray Firth, based on the interplay of internal motivational states. We use that model to estimate individual dolphins' exposure and motivational states during a 6 year baseline period, and then predict future changes in exposure and motivational states resulting from proposed industrial developments. Finally, we test whether there is any association between the estimated exposure of individual females to disturbance and the survival of their calves (figure 1).

2. Material and methods

(a) Individual-based model

We developed an individual-based model that combined the results of previous studies on dolphin ranging patterns in the Moray Firth [28], on spatio-temporal distribution of foraging activity [29], on the distribution of boat traffic [22,28] and on the effect of boat interactions [33] and construction activities [32] on dolphin behaviour (figure 1). The model-simulated dolphin behavioural dynamics under the assumption that each individual had a set of two motivational states (to acquire energy and to spend energy) that resulted from the integration of internal and external stimuli and that regulated its behavioural decisions [19,20]. Dolphin movements across their range were then determined on the principles of habitat selection and foraging theory. When the motivation to acquire energy was higher than the motivation to spend energy, we assumed that animals would try to meet their energy needs by preferentially selecting locations where they could find suitable foraging opportunities [34]. When their motivation to spend energy was higher, we used the observed pattern of habitat use in a given year to determine an individual's movements, on the assumption that the observed home range was the result of its attempts to meet its needs other than foraging (e.g. travelling, mating and other social interactions, resting or minimizing perceived risks). We assumed that dolphins perceived anthropogenic disturbance as a form of predation risk [15]. Therefore, any behavioural response would emerge indirectly from disturbance affecting the individuals' motivation to spend energy.

While building on the concepts developed in [22,23], our model shifts the focus to the habitat preferences and autonomous decision-making regarding movement and activity of individual animals. In addition, we replace the tuned parameters used in [22] with ecological parameters estimated from empirical data. The model is described using the updated overview, design concepts, details protocol [35,36]. The sections 'design concepts', 'initialization' and 'submodels' are provided in the electronic supplementary material, where model assumptions are also discussed. The code for constructing the individual-based model is included in the electronic supplementary material.

(i) Purpose

The purpose of our individual-based model was to simulate individual dolphins' behavioural dynamics, track their motivational states across time and assess the effect of exposure to boat traffic and construction activity on individuals' activity budget and motivations.
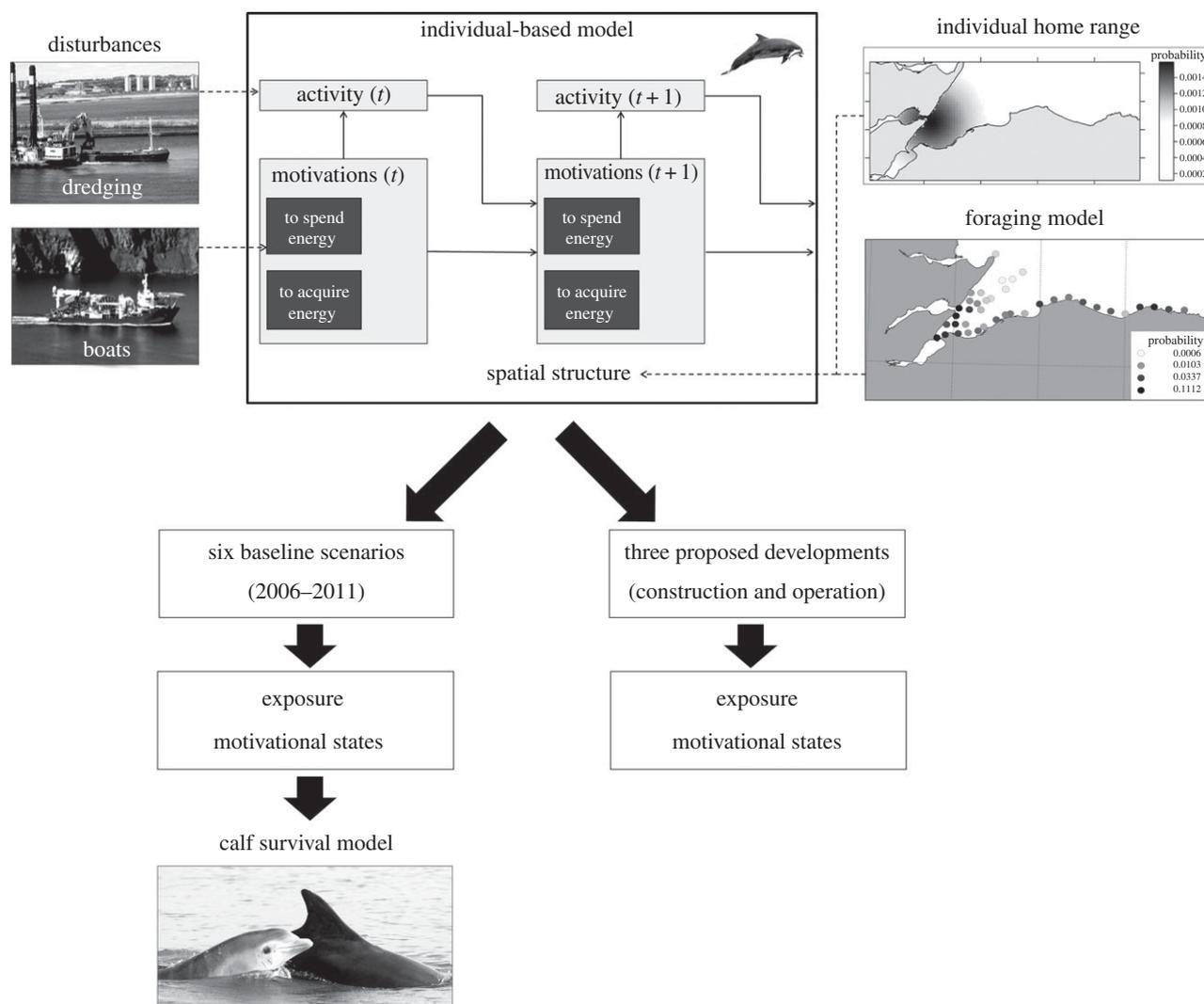
Figure 1. Conceptual diagram summarizing the study. Information on individual home ranges [28], distribution of foraging activity [29] and the effects of dredging activity [32] and boat interactions [33] informed an individual-based model for dolphin behavioural dynamics. This was used to predict individual exposure and motivational states under six baseline scenarios and one scenario with three proposed developments (all involving a construction and an operational phase). The effect of the predicted exposure and motivations of individual females on the survival probability of their calves was then tested using a multi-stage model.

(ii) State variables and scales

The model entities were individual dolphins and grid cells. Individual dolphins' state variables were: individual identification code, home range, motivational states, desired activity, actual activity, location, total number of boat interactions and daily activity budget (i.e. the percentage of time spent engaging in each activity). The motivational states of each individual dolphin were unitless measurements varying between −1 (indicating complete satisfaction with a motivation) and 1 (indicating complete dissatisfaction). We considered two competing motivations: the motivation to spend energy (i.e. to perform any activity that involves energy expenditure) and the motivation to acquire energy (i.e. to forage, because this is the only activity that warrants energy intake). These corresponded to two possible activities: acquiring energy and spending energy. Grid cells were characterized by their latitude and longitude, their daily suitability for acquiring energy, level of boat traffic (mean daily number of hours spent by boats in each cell) and presence or absence of dredging activities.

We simulated between 27 and 35 individual dolphins, depending on the year (electronic supplementary material, table S1). While individuals in this population range along the entire East coast of Scotland [26], we simulated only those that were known to spend most of their time in the inner Moray Firth area [31,37], and for whom an estimate of home range was available [28]. They included 17 known females. We used a grid of 959, 1 × 1 km cells enclosing

suitable dolphin habitat in the Moray Firth [28] (figure 2). For each simulation, the model was run 500 times for 612 discrete 6 h time steps, resulting in a time horizon of 153 days. Six hours was the mean duration of an activity bout, as indicated by the patterns of autocorrelation in the residuals of previous models of dolphin foraging in the area [29,33] (electronic supplementary material, figure S1). The 153 days covered the period between 1 May and 30 September each year, corresponding to the mark−recapture sampling period for this population.

(iii) Process overview and scheduling

A dolphin's desired activity at the beginning of each 6 h time step was determined by its motivational states: if the motivation to acquire energy was stronger (i.e. the value of this variable was more positive), the individual would want to acquire energy, and vice versa. A new spatial location was then drawn, based on the desired activity, the individual's home range and the availability of foraging opportunities on that day. Specifically, if the dolphin's desired activity was spending energy, it did so in a location drawn from its home range for the entire bout, and the motivational states were updated accordingly. We assumed that the selection of a new location did not depend on the locations of other individuals. If the desired activity was acquiring energy, a location was drawn from the foraging surface (a probability surface representing the likelihood of each cell being suitable for
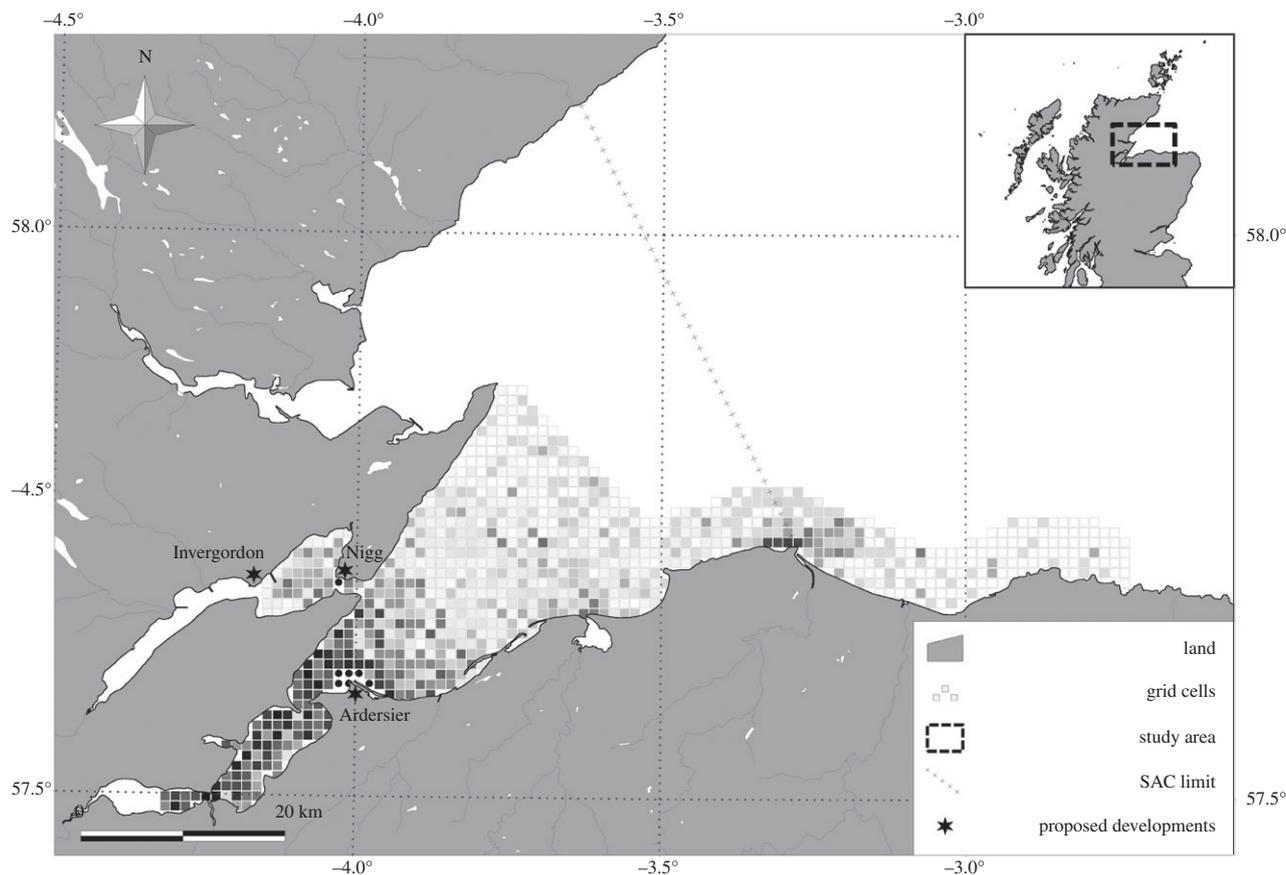
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Figure 2. Map of the study area. The grid cells are shaded based on the average daily boat hours over the summer (a darker shade corresponds to more intense traffic). Dotted cells indicate excluded locations when dredging was occurring at the development sites (indicated by a star).

foraging). If no suitable cell was found in the foraging surface, the individual would also spend energy for the entire bout. If a suitable cell was found, the 6 h bout was split into 120 3 min intervals (the median duration of a boat passage previously recorded in the area; [33]). The number of boats present at that location in a 3 min interval was based on a binomial draw from the total number of daily boat hours in the cell. We assumed that the change in foraging activity recorded by Pirotta et al. [33] derived from an increase in dolphins' motivation to spend energy as a result of interactions with boats (see 'Submodels' in the electronic supplementary material for details). If this motivation became greater than the motivation to acquire energy, the animal would not forage and would therefore spend energy in that interval. If the animals could successfully forage, this decreased the corresponding motivation. The number of intervals in which an individual interacted with boats was recorded. The mean activity budget was calculated at the end of each day (i.e. after four 6 h bouts). The predicted foraging surface was updated based on the available model [29] and the values of the environmental covariates in the following day. For each simulation, we recorded each individual's overall mean motivational states, its mean motivation states in the last week of the simulation (i.e. its final state), the number of times its motivations were completely satisfied or dissatisfied, the number of boat interactions and the mean activity budget. Details of the submodels and model equations are provided in the electronic supplementary material.

(iv) Input data
External inputs to the model included estimates of each individual's home range for the given year, the estimated spatio-temporal distribution of dolphin foraging activity, the predicted distribution of boat traffic across the study area under baseline and disturbed conditions, the estimated effect of boat presence and number on animals' motivations, and the estimated effect of dredging activities.

We modelled six baseline conditions, corresponding to the summers between 2006 and 2011. We used the estimated individual home ranges for each summer from Pirotta et al. [28], the dynamic distribution of foraging activity predicted as a function of environmental conditions from Pirotta et al. [29], and the number of boat hours predicted for each cell on each day by the boat model described in [22,28]. The distribution of foraging activity was used as a measure of the daily suitability of each cell for dolphin foraging, and was calculated using the model from Pirotta et al. [29] and the values of the environmental covariates on each day. The spatio-temporal distribution of boat traffic was assumed to be the same across different years (figure 2). Pirotta et al. [33] provided estimates of the effect of boat presence and numbers on foraging activity. We compared the number of boat interactions between years and individuals using a Poisson generalized linear model (GLM). The motivational states did not follow a Gaussian distribution. Therefore, we transformed the response by adding 1.0001, and used a gamma GLM to analyse the variability of the motivational states between years and individuals. This transformation was required, because the gamma distribution is bounded at 0 (not included), whereas motivations had a lower bound of −1.

We also simulated a series of disturbance conditions. In particular, we considered the construction and operational phase of three proposed coastal development sites in the area (port of Ardersier, Invergordon, Nigg Bay; figure 2). The details of these developments are provided in environmental statements that are available on the website of the Scottish Government (http://www.scotland.gov.uk/Resource/0041/00416136.pdf, http://www.scotland.gov.uk/Resource/0042/00423292.pdf and http://www.scotland.gov.uk/Resource/0043/00438787.pdf). A summary of the key activities associated with these developments is provided in the electronic supplementary material, table S3. They all involved an increase in boat traffic (which was integrated with the map of existing traffic) and some dredging, which was assumed to exclude the dolphins from grid cells within 1 km of the dredging site, on the basis of

Pirotta et al. [32]. These cells were removed from the home range in the periods when dredging was taking place. The developments also involved disposal of dredged material at sea and some piling activities, but these could not be included in the model because of the absence of data on the animals' potential responses. The effects of construction and operation of the three sites were modelled using the environmental conditions and individual home ranges observed in 2009 and 2010, because previous work showed that these years reliably exemplified different dolphin ranging patterns among the 6 years analysed [28].

(v) Simulated population scenarios

We simulated three scenarios of population status to calibrate the individual-based model parameters. These scenarios were based on the mean individual motivational states at the end of the simulated summer season under mean home range and foraging conditions and with a baseline condition of boat traffic (see the electronic supplementary material):

scenario 1: all individuals were completely satisfied with their motivational states (i.e. their motivational states were close to -1);

scenario 2: individuals were on average satisfied with their motivational states (i.e. the mean value of the motivations was -0.5); and

scenario 3: on average, individuals were not satisfied nor dissatisfied with their motivational states (i.e. the mean value of the motivations was 0, and the population was therefore on the verge of a possible decline caused by its individuals not being able to meet their needs).

(b) A multi-stage model for calf survival

We tested whether the exposure to boat traffic and the motivational states of individual females estimated by the individual-based model had an effect on their ability to successfully raise their calves, i.e. if they affected calf survival probability. We used model predictions in the six baseline years in association with information from long-term photo-identification studies carried out in the Moray Firth SAC [38] and in the southern part of the population's range [37]. On average, 28 (Moray Firth SAC) and 12 dedicated surveys (southern part of the range) were conducted each summer (May–September) in the study period (2006–2011). The studies record the occurrence of each identified dolphin in the study area and whether or not they were accompanied by calves. We focused on the sighting history of calves that were consistently associated with the same female [39], because we anticipated that disturbance was more likely to affect calf survival rather than female pregnancy rate [40,41].

Details of the photo-identification data collection are provided in [26,27,37]. We developed a multi-stage model of calf history, where each calf could transition between four different stages:

— stage 1: newborn (age 0, born in that same year);
— stage 2: age 1 or 2 years;
— stage 3: age 3 or more; or
— stage 4: dead.

We grouped calves of age 1 and 2 together in order to reduce the number of parameters in the model, and because we expected calves to be at least partially dependent on maternal milk until at least the age of 3 [42]. Because calves could be lost once the association with their mother loosened (owing to the limited amount of marking on their fins), we decided to introduce an observation model under which the calf's stage could be misclassified. In particular, a calf that was classified as dead could, in reality, be in stage 2 or 3 but unrecognized. We considered the sighting histories of 20 calves that were associated with 14 females included

in our individual-based model (i.e. females for which we had information on exposure to disturbance) during 2006–2012 (electronic supplementary material, table S2). We tested for an effect of the predicted exposure to boat interactions across the summer, the mean and final motivation to acquire energy, and the number of maternal satisfactions and dissatisfactions with the motivation to acquire energy experienced by the females on the transition of the dependent calf to the subsequent stage. We fitted the hierarchical model in a Bayesian framework. Additional analytical details and assumptions are provided in the electronic supplementary material.

Given the small sample size available to inform the multi-stage model, we designed a simulation study to assess the bias on the estimates of the transition probabilities and the effect size required to retain the effect of boat exposure. Further details on the simulation study are provided in the electronic supplementary material.

3. Results

(a) Individual-based model

The estimated mean and final motivational states for the years 2006–2011, as well as the number of satisfactions and dissatisfactions, confirmed the expected differences between the three population status scenarios resulting from the adjustment of the cost–benefit parameters (electronic supplementary material, figures S2–S5). Differences between years were much smaller, although the Poisson GLM showed that the number of boat interactions changed significantly ($\chi_5^2 = 310\,727$; $p < 2.2 \times 10^{-16}$). The model also highlighted significant differences between individuals ($\chi_{34}^2 = 111\,376$; $p < 2.2 \times 10^{-16}$). The motivations were found to vary consistently among years (e.g. mean motivation to acquire energy: $\chi_5^2 = 5654$; $p < 2.2 \times 10^{-16}$) and among individuals (e.g. mean motivation to acquire energy: $\chi_{34}^2 = 1600$; $p < 2.2 \times 10^{-16}$).

The model did not predict any substantial change in either the overall exposure of the animals or their motivational states as a result of the increase in boat traffic and dredging activity during the construction phase of the three development sites (figure 3 and electronic supplementary material, figures S6 and S7). However, during the operational phase, a relatively small increase in the number of boat interactions experienced by each individual across the summer (median difference = 9 (scenario 1)–16 (scenario 3)) was sufficient to cause a shift of the motivational states towards dissatisfaction (figure 3 and electronic supplementary material, figures S6 and S8). This increase was more evident under scenario 3, in which the population was on the verge of a possible decline caused by its individuals not being able to meet their needs (mean difference in mean motivation to acquire energy = 0.19), than under scenario 1, in which individuals were completely satisfied (mean difference = 0.003). In particular, the mean across the 500 simulations became greater than zero, suggesting overall dissatisfaction for both motivational states. We did not detect any relevant difference between the predicted scenarios run using 2009 versus 2010 ranging patterns in either the construction or operational phases.

(b) Calf multi-stage model

The Markov chain Monte Carlo (MCMC) chains quickly converged and there appeared to be no issues with autocorrelation. The effects of the number of boat interactions on the transition probabilities between stages were found to be
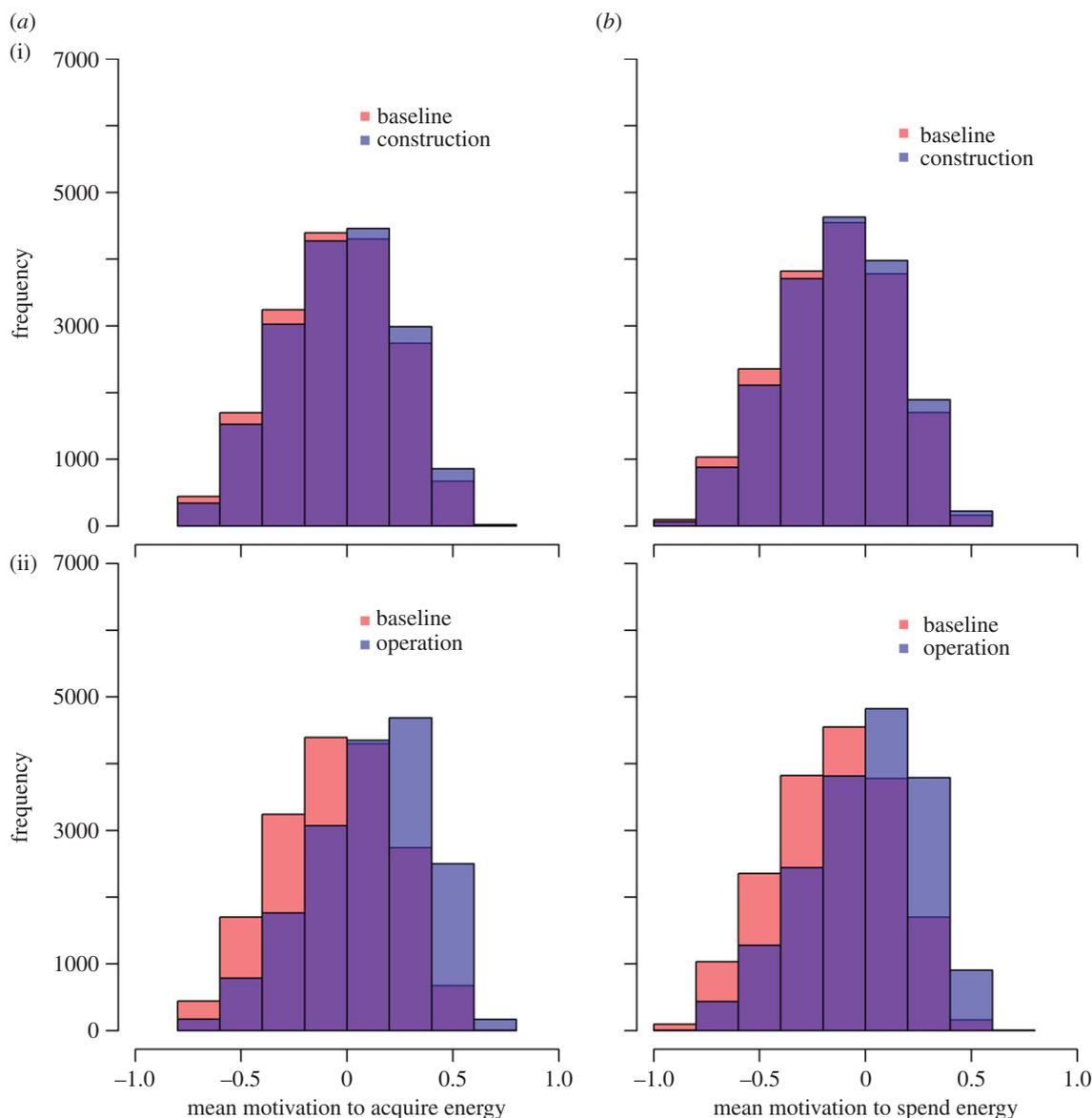
Figure 3. Distribution of the mean motivation to acquire energy (*a*) and mean motivation to spend energy (*b*) of individual dolphins under baseline conditions and during construction (i) and operation (ii) for scenario 3 of population status. 2009 was used here as the baseline condition. (Online version in colour.)

negligible, based on the mean values of the corresponding indicator variables ($w_{\beta 1} < 0.5$; $w_{\beta 2} < 0.5$). The result did not change when effects on the mean and final motivation to acquire energy were tested. Therefore, we concluded that there was no detectable association between the mothers' predicted exposure and motivational states and the survival of their calves. We removed these effects from the model and re-ran the MCMC. The resulting matrix of posterior transition probabilities was

$$\mathbf{P} = \begin{bmatrix} 0 & 0.87 & 0 & 0.13 \\ 0 & 0 & 0.73 & 0.27 \\ 0 & 0 & 0.84 & 0.16 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

show a high probability of surviving to age 1 (p_{12}). The matrix of posterior misclassification probabilities for the observation model was (electronic supplementary material, table S4)

$$\mathbf{Pm} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0.95 & 0 & 0.05 \\ 0 & 0 & 0.95 & 0.05 \\ 0 & 0 & 0 & 1 \end{bmatrix}.$$

4. Discussion

Effective management of human developments in the marine environment requires an approach that protects marine mammal populations while allowing for the sustainable use of marine resources. Human activities do not necessarily lead to the direct injury or death of the exposed individuals, but sublethal changes in individual behaviour can result in changes in individual vital rates, mediated by the alteration of the animals' energy balance and condition [8,10–12]. Similar behaviourally mediated cascading effects have been observed in response to variation in the spatio-temporal patterns of predation risk, which can cause substantial changes in an entire community [14]. It is therefore important to develop analytical frameworks that allow such effects to be predicted before the population declines, in order to inform effective regulation of anthropogenic disturbances [8]. Here, we describe a model framework, constructed using a robust evidence base, that can be used to address these issues and facilitate management decisions.

We developed an individual-based model for bottlenose dolphin behavioural ecology that combines previous

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individual- and population-level empirical observations to inform the animals' unobservable motivational states. Our work builds on similar approaches developed for this and other dolphin populations [22,23], but, crucially, our focus is on individuals rather than schools. We used information on the ranging pattern of a selection of well-known individual animals to estimate their spatially explicit exposure to disturbance and to make predictions of their state. The heterogeneity in home ranges and, consequently, exposure was assumed to be representative of the portion of the population consistently using the study area, and thus provide an estimate of the range of potential effects on the individuals, even when the mean effect is overall negligible. Understanding the variability around the absence of an effect is critical if any long-term population trend is to be predicted, because the contribution of different individuals to the demography of the population might be unbalanced [43,44].

Our individual-based model represents a useful framework for making informed predictions about the individual consequences of changes in exposure resulting from future developments. Here, we considered three proposed developments and their potential effects during both the construction and the operational phase on a local population of bottlenose dolphins. We showed that no detrimental effect is predicted following the increase in boat traffic and dredging activity during the construction phase, although we were not able to consider the potential effects of piling and disposal of dredged material. However, increases in traffic during the operational phase could cause a change in the motivational states of the individuals, with potential consequences on the individuals' condition and, ultimately, vital rates. This effect, and its relevance from a management perspective, is likely to be strongest if the population is close to a tipping point between stationarity and decline. In these circumstances, the overall population is more likely to move into a situation where individuals cannot satisfy their motivational states. At the moment, we have no means to assess where the mean motivation in the population lies on this continuum, and therefore, we cannot make predictions of the population's ability to compensate for these potential changes.

In the absence of data on the current mean motivational state of the population, we simulated three possible underlying scenarios. Therefore, our results represent a gradient of increasing precaution that takes account of known uncertainties and whose predictions are relatively easy to communicate to decision-makers. However, in order to ensure the favourable conservation status of the population, estimates of motivational states need to be translated into measures of individuals' demographic contributions [8]. Developing a bioenergetic model to predict changes in individual condition would require an unreasonable number of assumptions, as few data are available on the diet and energetic strategies of this population, or on prey availability and distribution. Rather than introducing additional uncertainty, we decided to ignore intermediate changes in condition and directly investigate the link between disturbance and calf survival. We used a Bayesian multi-stage model to assess whether the exposure and motivational states of the mothers could have a detectable effect on the transition of their calves between critical growth stages. We were unable to detect any significant effect, which is not surprising given the small sample size compared with the expected individual differences in reproductive output [42,44]. In addition, the overall stability of the population size

[27] implies that any current detrimental effect on calf survival is probably small.

We carried out a simulation study to identify the sample size required to obtain unbiased estimates of the relevant probabilities, and the minimum detectable effect size (electronic supplementary material). We showed that even in this well-known population, the information we have might not be sufficient to detect an effect. At least two to four times the number of calf histories than currently available is needed to obtain reliable estimates (with bias < 5%) of these parameters. For example, in our sample, only one calf died in the first year, which led to an overestimation of the corresponding transition probability, as some newborn calves might have been born and died before there was an opportunity to capture them photographically [37]. An increased sample size could be achieved by tracking the same females for longer or by including more females in the analysis. Including more females would be better to avoid issues with non-independence of the histories of calves generated by the same mother. In both cases, though, additional data on females' ranging patterns are required. Previous work on elephant seals has shown that it is more effective to characterize the mechanisms that link disturbance to females' lipid gain and condition, and lipid condition to pup condition and survival [8]. In terms of future research investments, it may therefore be more cost-effective to focus on the parametrization of the intermediate links, rather than waiting to have a large enough sample size (or a bad enough effect) for the calf survival model to retrieve unbiased estimates. However, the model could provide a temporary alternative in larger populations.

The trajectory of this bottlenose dolphin population is currently stable [26,27] and, despite the biases deriving from the small sample size, the simulation study suggested that the proposed developments are unlikely to cause a substantial disruption of calf survival (or, at least, the effect cannot be distinguished from natural individual heterogeneity). In the light of these results, the condition of individuals should now be monitored, so that any deterioration following increased exposure to disturbance can be rapidly detected, before it translates into longer-term changes in the population's trend. The growth rate of immature animals and the accumulation of energy stores in the blubber could represent good proxies of individual condition, but new techniques to measure them at sea are required. We are currently investigating photogrammetric methods to estimate calf growth [45,46]. Research is also ongoing to identify a suitable technique to estimate blubber stores from photographic data, as has been done for pinnipeds [47]. In addition, accelerometry data collected by electronic tags have been used to estimate pinnipeds' body condition and its variation at sea [48,49]. While accelerometer sensors have been successfully combined with suction-cap tags for free-ranging cetaceans [50], future research should aim at improving attachment techniques to allow for longer-term sampling than is currently possible and for more effective remote transmission of the data. Capture and release of wild animals for direct measurements is possible at a small number of sites, where some of these indirect techniques could be validated [46].

The effect of other disturbances, which will occur concurrently to dredging and increased boat traffic, should also be considered. For example, the construction phase will include pile-driving activities, and, to date, we have no empirical information on dolphin responses to this source of disturbance,

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beyond the potential auditory damages it could cause at close range. The disposal at sea of material that has been dredged may also have unknown consequences for behaviour. Our framework integrates the effects of various activities on the population and could be extended to these additional disturbances, once information on the corresponding behavioural response of the animals becomes available, and the risk of injuries. Modelling cumulative effects is crucial for guiding management decisions in complex systems, where it is unclear which impacts exert the highest pressure on wildlife [51]. The issue of possible synergies between different impacts also remains to be investigated.

Given the difficulties in quantifying some of the functional links in a setting where we have a robust ecological understanding of the population of interest and a large dataset spanning over two decades, the question remains as to which cetacean population may offer a sufficiently detailed case study for a complete parametrization of a framework predicting the long-term effects of disturbance on population dynamics [8,9]. There are stable inshore populations of cetaceans where even more detailed data are available, for example the population of bottlenose dolphins resident in Sarasota Bay, Florida [52,53]. However, the scientific community should first explore whether and how the values of any parameter estimated in a specific context can be robustly extrapolated to other unsampled or less known species, where tolerance towards disturbance could also vary. For example, it could be assumed that species with comparable life histories will adopt the same strategies in response to a disturbance source or a changing habitat, and will make similar decisions to allocate their energy. Marine mammal reproductive strategy is often placed along a continuum ranging from capital breeding, in which individuals rely on stored reserves during the reproductive period, to income breeding, in which individuals have to forage during lactation [54]. Our framework was developed for an income breeding species, but the idea of underlying motivations driving the engagement in observable activities can also be applied to a capital breeder on its feeding ground [55].

5. Conclusion

Approaches that link short-term physiological and behavioural responses to disturbance to long-term population consequences could provide an overarching framework for investigating wildlife populations' viability in a changing environment [8,9,56]. We show how information on the behavioural ecology of a population can be integrated into an individual-based model that predicts an individual's behavioural dynamics and any potential change in its vital rates resulting from disturbance. This model could easily be adapted to other small populations of marine mammals where similar information has been collected. While some mechanistic links still need to be appropriately informed, our work can be used to guide management decisions, accelerate the consenting process for coastal and offshore developments, and identify knowledge gaps that need to be filled using appropriate monitoring methods.

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