

The importance of spinner dolphin (*Stenella longirostris*) resting habitat: implications for management

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Summary

1. Linking key ecological characteristics with animal behaviour is essential for identifying and protecting important habitats that support life functions. Spinner dolphins display a predictable diurnal behavioural pattern where they forage offshore at night and return to sheltered bays during daytime to rest. These bays, which are also subject to considerable use by humans, have long been recognized as key habitats for this species although the extent to which dolphins rely on specific characteristics of these habitats for rest has not been quantified.

2. An integration of boat-based and land-based group focal follow sampling regimes and three gradient boosting generalized additive models were developed to identify habitat features that contribute to the occurrence of resting spinner dolphins in coastal waters off Hawai'i Island. Two 'in-bay' models used data collected within bays, and a third 'coastal' model (near-shore, outside of bays) used data collected both inside and outside of bays.

3. The coastal model identified that spinner dolphins were unlikely to rest outside sheltered bays. In-bay models showed that dolphins rested throughout daylight hours within bays with a peak resting period between 10.00 h to 14.00 h. The models also identified bottom-substrate-type as an important predictor of rest. Pseudo R^2 values of 0.61 and 0.70 for the in-bay models and 0.66 for the coastal model showed that these models provided a good fit to the behavioural data for the occurrence of resting spinner dolphins.

4. *Synthesis and application.* To date, studies evaluating spinner dolphin resting habitat have focussed on areas inside bays only. Here, we combined data collected inside and outside bays, and illustrate that should resting spinner dolphins be displaced from resting bays, they are unlikely to engage in resting behaviour elsewhere. Results provide further information on the importance of bays as important habitat for resting spinner dolphins. To mitigate the disturbance from human interactions during important rest periods, we recommend that management keep the spinner dolphin resting areas free from human activities. Our quantitative approach where models explicitly link behaviour with habitat characteristics is applicable to identify important habitats for protection of other taxa.

Key-words: behaviour, conservation, gradient boosted generalized additive models, Hawai'i, marine protected areas, science-informed management, tourism impacts

Introduction

Animals choose between behavioural activities across time and space (habitat) to optimally exploit resources such as prey (Heithaus & Dill 2002) and shelter (Lima 1998) and

to avoid predators (Heithaus *et al.* 2008). The costs and benefits associated with choosing one behaviour over another shapes the evolution of behavioural strategies which, in turn, influence individual fitness (Dill 1987; Lima & Dill 1990). Identifying relationships between behaviour and ecology is challenging as they vary over space and time (Dill 1987). Spatially, these relationships

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exist over distances varying from a few metres to thousands of kilometres and, temporally, over hours to months (Corkeron *et al.* 2001; Armstrong *et al.* 2013).

Key habitats may function as critical for population viability by providing optimal resources (e.g. shelter, prey) (Dill 1987). In addition to coping with environmental variations and resource availability within key habitats, many animals must also cope with the consequences of human disturbance, including climate change (Johnston *et al.* 2012), deforestation (Johnson, Seip & Boyce 2004), development (Holdo *et al.* 2011), overfishing (Worm *et al.* 2013), bycatch (Allen *et al.* 2014) and tourism (Constantine, Brunton & Dennis 2004; Bejder *et al.* 2006b; Lusseau, Slooten & Currey 2006). To quantify potential negative impacts of human disturbance on animal populations, important areas for population viability can be identified by linking habitat characteristics to either animal presence (Goetz *et al.* 2012) and/or important life functional behaviours (Lusseau & Higham 2004). Critical habitats can be defined as areas where animals exhibit important behaviours such as foraging, breeding, nursing, socializing and resting (Lusseau & Higham 2004; Hoyt 2011).

Hawaiian spinner dolphins (*Stenella longirostris*) exploit sheltered bays to socialize and rest during the day, following a night of cooperative foraging in open-water foraging grounds (Norris *et al.* 1994; Benoit-Bird & Au 2009). This temporal partitioning of behaviours allows spinner dolphins to maximize their foraging efficiency while minimizing predation risk during periods of rest (Norris *et al.* 1994; Benoit-Bird & Au 2009). This predictable behavioural pattern makes spinner dolphins vulnerable to perturbation during rest periods, especially if they are unable to compensate for disrupted resting periods (Johnston 2014). The Hawai'i Island associated spinner dolphin population may be especially vulnerable to human disturbance because their resting habitats are subject to considerable human activity (Heenehan *et al.* 2014), the population is small (Tyne *et al.* 2014) and genetically isolated (Andrews *et al.* 2010).

Specifically, sheltered bays used by spinner dolphins to rest are also used by people for recreational and commercial purposes (Heenehan *et al.* 2014). Spinner dolphin resting periods are interrupted or truncated by exposure to human activity (Courbis & Timmel 2009), and they are less likely to rest when swimmers are within 150 m (J. Symons, J.A. Tyne, L. Bejder, D.W. Johnston & D. Lusseau, unpublished data).

The US National Oceanic and Atmospheric Administration (NOAA) is mandated to protect all cetaceans, seals and sea lions in US waters, including the protection of 'essential habitat, including rookeries, mating grounds, and areas of similar significance for each species of marine mammal from the adverse effect of man's actions.' (MMPA 1972). Evidence suggests that protected areas can be effective for marine mammal conservation if of appropriate size (Gormley *et al.* 2012; Edgar *et al.* 2014). NOAA is considering several management strategies to

mitigate the negative effects of human–spinner dolphin interactions (NOAA 2005), including the use of area closures to reduce the number and intensity of interactions during dolphin resting periods. This strategy proposes to identify specific areas that are important to the population's survival and restricting human access (Tyne, Lone-ragan & Bejder 2014).

We combined boat-based and land-based group focal follow data to determine the resting behaviour of spinner dolphins across a range of available habitats, inside four bays and along open coastline adjacent to the bays. Our specific objectives were to (i) identify key habitat factors that contribute to the likelihood of spinner dolphin rest, and (ii) determine time periods that the spinner dolphins are most likely to rest within these habitats.

Materials and methods

Along the Kona Coast (between 19° 55' 37"N, 155° 53' 45"W and 19° 21' 40"N, 155° 53' 31"W) on the leeward side of Hawai'i Island (Fig. 1), spinner dolphins are often observed within four bays during daylight hours (Makako Bay, Kealakekua Bay, Honaunau Bay and Kauhako Bay, Fig. 1) (Norris *et al.* 1994; Thorne *et al.* 2012; Tyne *et al.* 2014). Land-based and boat-based group focal follows collected behavioural data on dolphin groups both inside and outside (within 1 km of the coastline) these four sheltered bays.

GROUP FOCAL FOLLOWS

Established group focal follow protocols were employed to collect positional and behavioural information on spinner dolphins during daylight hours from both boat-based and land-based platforms (see Table S1, Supporting Information). Group focal follows often consist of a combination of continuous and scan sampling procedures (Altmann 1974; Mann 1999). Continuous sampling was used to obtain all occurrences of specific dolphin behavioural events. Instantaneous scan sampling was used to record predominant group behavioural activity at regular intervals, for example resting and socializing (Altmann 1974; Mann 1999; Bejder *et al.* 2006a).

A spinner dolphin group was defined using a 100-m chain rule: when A is within 100 m of B and B is within 100 m of C but A and C are more than 100 m apart, A and C are considered to be in the same group (modified from Smolker *et al.* 1992). Continuous sampling was employed to record all occurrences of fission–fusion events by individuals of the focal group. A fission event was defined as when an individual, or part of the group, moved beyond the 100 m chain, and a fusion event was defined as when they joined the focal group by moving within the 100 m chain. Instantaneous scan sampling protocols were employed at 5 (boat-based) and 10-min (land-based) intervals to record the predominant group activity of the majority ($\geq 50\%$) of individuals in the focal group, group size (minimum, best and max group size estimates) and dolphin group location. A minimum of four researchers continuously tracked spinner dolphins during a group focal follow. An observation period was terminated when the behaviour of the dolphins could no longer be reliably determined because of events, such as poor visibility, dolphins moved out of range or dolphins split into too many groups.

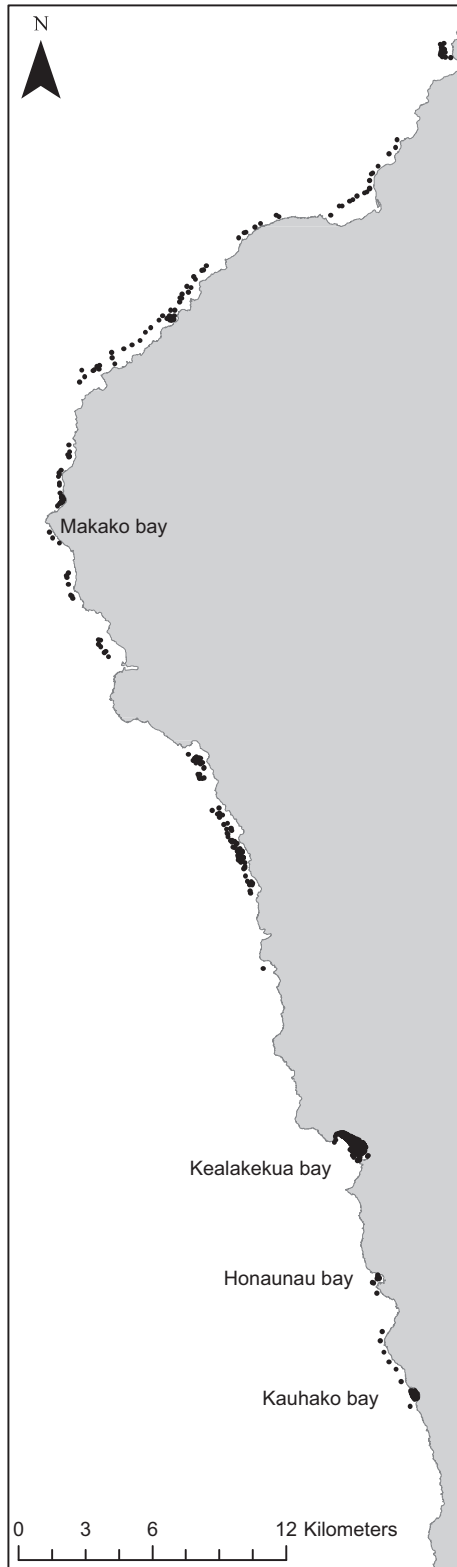


Fig. 1. The location of the spinner dolphin study area on the Kona Coast showing the four sheltered bays: Kauhako Bay, Honaunau Bay, Kealakekua Bay and Makako Bay, Hawai'i Island, and the behavioural observations of spinner dolphin groups (black circles) recorded during boat-based ($n = 28$) and land-based ($n = 47$) group focal follows. Each black circle ($n = 2856$) corresponds to the location where each 10-min scan sample was obtained.

LAND-BASED GROUP FOCAL FOLLOWS

Land-based group focal follows were undertaken from high vantage points overlooking Kealakekua Bay (139 m, $19^{\circ} 28' 59.7''$, $155^{\circ} 55' 51''$) and Kauhako Bay (57 m, $19^{\circ} 22' 44.5''$, $155^{\circ} 53' 47.5''$). A SOKKIA DT5-10 digital theodolite equipped with a $30\times$ lens was connected to a laptop computer running the computer program PYTHAGORAS (Gailey & Ortega-Ortiz 2002). PYTHAGORAS used data on the theodolite's position, height above sea level (including tidal fluctuations) and a reference point used for zeroing, to convert theodolite positional fixes of target objects (dolphin groups, boats, swimmers, kayakers) into latitudinal and longitudinal coordinates (Würsig, Cipriano & Würsig 1991). At the start of tracking (usually between 06:30 am and 07:00 am) and at hourly intervals, a scan was carried out to fix the position of all vessels, swimmers and kayakers in the bay. A positional fix was taken of the focal dolphin group every 5 min, and the predominant group behaviour was recorded every 10 min. Theodolite observations were not carried out at Honaunau and Makako bays because of insufficient elevation to reliably track dolphins from land.

BOAT-BASED GROUP FOCAL FOLLOWS

A 7-m research vessel equipped with a 90-hp four stroke outboard, left dock at sunrise, with a minimum of four researchers on board to look for spinner dolphin groups moving inshore from their night-time foraging grounds. The vessel travelled within 1 km of the coast until spinner dolphins were located. Continuous and instantaneous scan samplings were then initiated to document group behavioural information. The predominant group activity was recorded every 5 min. Using logger 2000 (IFAW software), GPS coordinates of the focal group were recorded at 30 s intervals. Fission–fusion events were recorded continuously during the sampling period. To minimize the impact of the presence of the research vessel on the spinner dolphins during group focal follows, the vessel was maintained at a distance of approximately 100 m from the focal group and was positioned behind and to the side of the group. All care was taken to minimize disturbance and changes in the dolphin group behaviour induced by the presence of the vessel.

BATHYMETRIC AND BENTHIC DATA

Bathymetric and benthic habitat data were produced using high-resolution satellite, LiDAR (light detection and ranging) and acoustic SONAR (sound navigation and ranging). These data were downloaded from the Centre for Coastal Monitoring and Assessment website (<http://coastalscience.noaa.gov/>) with a resolution of $50 \times 50 \text{ m}^2$. Focal follow data were converted from latitude and longitude projection to the Universal Transverse Mercator (UTM) coordinate system and overlaid upon the bathymetric and habitat maps using ArcGIS 10.1; Environmental Systems Resource Institute, Redlands, CA, USA. Maps were overlaid on a grid divided into 50 m^2 cells. Thereafter, the corresponding depth, distance from shore, habitat type, position and time-of-day for each 10-min dolphin group behavioural sample in each cell were extracted and exported to an Microsoft Access data base. The land-based focal follow protocol collected data every 5 min. However, alternate data points were removed so that these data matched the boat-based protocol. For some

behavioural observations, habitat type and depth could not be determined from the remotely sensed bathymetric and benthic habitat data. These data were removed from the modelling process.

MODELLING APPROACH

We employed a method for addressing the complexities of nonlinear and autocorrelated ecological data commonly referred to as component-wise gradient boosting (Friedman, Hastie & Tibshirani 2000). Component-wise gradient boosting is a machine learning method for obtaining statistical model estimates via gradient-descent techniques (Friedman, Hastie & Tibshirani 2000; Hastie, Tibshirani & Friedman 2009). Binomial component-wise gradient-descent boosted generalized additive models (GAMs), hereafter referred to as boosted GAMs, were used to explore the relationship between resting spinner dolphins and a number of environmental, spatial and temporal factors inside and out of the four sheltered bays along the Kona coast of Hawai'i Island. Boosting allows an integrated method for fitting constrained models with multiple sources of variation, including smooth spatial interdependence by using spatial splines, as well as other nonlinear functions of environmental covariates. We fitted a spatial spline in order to account for variance that is purely spatial and not related to the other covariates which is considered by Hothorn *et al.* (2010b) as a way to partially address spatial autocorrelation. Spinner dolphin behaviours were collapsed into a binomial response for behaviour states, that is resting and nonresting (1 and 0, respectively). The R software (R Core Team 2014), the boosting package 'MBOOST' (Hothorn *et al.* 2010a) and 'RODBC' (Ripley 2013) package were used to develop the boosted GAMs.

BASE-LEARNERS

Each predictor was added to the models via effect functions known as base-learners (for details see Hofner 2011). Bootstrapping and cross-validation were used to determine the optimal number of boosting iterations to provide maximum prediction accuracy and, in combination with automatic predictor selection, to prevent over-fitting (Hofner *et al.* 2014). Stability selection was used to determine the probability of predictor selection during the model-fitting process (Meinshausen & Bühlmann 2010).

Three models were developed to investigate the relationship between resting spinner dolphin groups and environmental, spatial and temporal factors. Two models used data collected inside Kauhako Bay and Kealakekua Bay ('in-bay models'), respectively, while the third model ('coastal model') used data collected both inside and outside of four sheltered bays: Kauhako Bay, Honaunau Bay, Kealakekua Bay and Makako Bay. Models developed for data collected inside Honaunau Bay and Makako Bay were unable to converge due to insufficient data from inside the bays, and they were therefore not included in further analysis. The two in-bay models were implemented using six base-learners, while the coastal model included a seventh base-learner and an interaction (Table 1). A maximum number of 1000 iterations were applied to each bootstrap. The optimal number of iterations was then determined, and the base-learners that contributed to the model fit in order of importance were identified from their selection frequencies and probabilities of selection. Marginal function plots were used to illustrate the relationship between the

Table 1. List of base-learners used in the three boosted generalized additive models (GAMs) to explore relationships between resting spinner dolphins (resting or nonresting) and environmental, spatial and temporal factors. Single bay models = Kealakekua Bay and Kauhako Bay; coastal model includes all bays and coastal waters

Model	Base-learners
All models (single bay and coastal model)	Substrate (sand, aggregate coral, rock/boulders) Depth (m) – mean centred Distance from shore (m) – mean centred Spatial position (converted to Universal Transverse Mercator) Time-of-day (morning: 6 am–10 am; mid-morning: 10 am–2 pm; afternoon: 2 pm–6 pm) Behavioural state during previous scan observation (resting/not-resting)
Coastal model	Inside or outside bays

response and the predictor variables after accounting for all other covariates (Maloney, Schmid & Weller 2012).

For each model, 50 bootstrap samples from the full data set were used as a training data set to which gradient boosting was applied, from which the pseudo R^2 (Nagelkerke 1991) was estimated. Predicted responses were back-transformed to their original measurement scales and used to produce predicted probability maps of resting spinner dolphin groups in Kauhako Bay and Kealakekua Bay.

Results

EFFORT AND SAMPLE SIZES

A total of 488 h of group behavioural data were collected during boat-based ($n = 121$ h) and land-based ($n = 367$ h) focal follows, with 402 h of observations (82.4%) made inside bays and 86 h outside of bays (Table 2). This resulted in 2856 observations of spinner dolphin behav-

Table 2. Number of focal follows, focal follow hours and mean focal follow duration from land-based and boat-based group focal follows of spinner dolphins inside bays and outside of bays along the Kona Coast, Hawai'i Island

Focal follow	Number of focal follows	Focal follow hours	Mean focal follow duration (hh:mm)
Land-based			
Kealakekua Bay	40	329	8:31 ± 0:19 SE
Kauhako Bay	7	38	3:25 ± 1:17 SE
Total	47	367	7:40 ± 0:22 SE
Boat-based			
Honaunau Bay	4	21	5:15 ± 1:24 SE
Makako Bay	4	14	3:26 ± 0:27 SE
Outside Bays	20	86	4:18 ± 0:33 SE
Total	28	121	4:20 ± 0:27 SE
Overall total	75	488	6:30 ± 0:20 SE

our (2395 inside bays and 461 outside bays; Fig. 1). The proportion of substrate types available to spinner dolphins in the study area varied inside and outside bays. However, the highest proportion was rock/boulder, followed by sand and then aggregate reef both inside and outside bays (see Table S2). Spinner dolphins predominantly rested inside bays (see Fig. S1) while predominantly travelled outside bays (see Fig. S2). Although the highest proportion of substrate available to spinner dolphins inside and outside bays was rock/boulder, spinner dolphins occurred disproportionately more over sand than any other substrate, 54% inside bays and 38% outside bays.

BOOSTED GAMS

The boosted GAM was used to take into account autocorrelation in the focal follow data. Since depth and substrate data could not be determined from the remote sensed bathymetric and habitat maps for some of the dolphin group observations, 406 and 102 data points were removed from inside and outside bays, respectively. This resulted in 2348 behavioural, depth and substrate data observations being included in the modelling procedure.

The prediction accuracy determined by the mean pseudo R^2 values for the models to predict the resting state of spinner dolphins was >0.6 for all models (0.701, 0.655–0.734 and 0.613, 0.608–0.617 for the two in-bay models; 0.663, 0.660–0.664 for the coastal model). These models provided a good fit to the behavioural data as pseudo R^2 values of between 0.55 and 0.60 have been described as moderate/good (Maloney, Schmid & Weller 2012). Locations, behaviour during previous scan observation and time-of-day were the most important variables for predicting resting behaviour of spinner dolphins in both the in-bay models (Table 3). For the coastal model, the inside/outside variable was the most influential variable in the model, with the time-of-day, behaviour during previous observation and the inside/outside bay \times sub-

strate interaction having a similar level of influence to each other (Table 3). No other predictor interactions were influential in predicting spinner dolphin group resting behaviour in the three models.

The coastal model indicated that spinner dolphin groups are unlikely to rest when outside sheltered bays (Fig. 2). When inside the bays, substrate was influential in predicting resting behaviour (Table 3). Depth and distance from shore were never selected as main predictors for any of the three models. Time-of-day was selected for all three models, which predicted that spinner dolphins had a higher probability of resting in the mid-morning than in the morning or afternoon (Fig. 3). In addition, spinner dolphin groups in Kealakekua Bay and Kauhako Bay predominantly rested over a sandy substrate (Fig. 4).

Discussion

The gradient boosted GAM analytical approach was used to identify factors that influence the resting behaviour of spinner dolphins. Boosting automatically selects variables and reduces effect estimates towards zero, which in combination avoids over-fitting (Hothorn *et al.* 2010b). Model fitting is constrained by stopping the model-fitting process at the optimal number of boosting iterations. This approach was used in preference to maximum-likelihood estimates that can over fit models when there are many predictors and complex spatial and temporal processes. Spatial autocorrelation was addressed by fitting a spatial spline to fit variance that is purely spatial and not related to the other covariates (Hothorn *et al.* 2010b).

The results confirm that four sheltered bays (Kauhako Bay, Honaunau Bay, Kealakekua Bay and Makako Bay) along the Kona Coast are important resting habitat for spinner dolphins during daylight hours. Although dolphins spent significant proportions of time resting in bays throughout daylight hours, most rest occurred between 10 am and 2 pm. This study expands on previous research that highlighted the importance of sheltered bays to spin-

Table 3. The variables selected during the boosted generalized additive models process to examine the influence of spatial position, previous behaviour, time-of-day, substrate and inside or outside of bays on the resting state of spinner dolphins. Optimal m is the point at which the model is stopped during the model-fitting process to avoid over-fitting. Stability selection shows the probability of variable selection at optimal m . Maximum iterations = 1000 bootstrap iterations with a 50-fold cross-validation

Model	Optimal m	Variables and selection frequencies	Stability selection probability at optimal m
(a) In-bay 1 ($n = 200$)	234	Spatial position	0.67
		Previous behaviour	0.25
		Time-of-day	0.06
(b) In-bay 2 ($n = 1596$)	223	Spatial position	0.52
		Previous behaviour	0.31
		Time-of-day	0.17
(c) Coastal ($n = 2348$)	431	Inside/outside bays	0.30
		Inside/outside bays + substrate	0.26
		Time-of-day	0.16
		Previous behaviour	0.15
		Spatial position	0.12

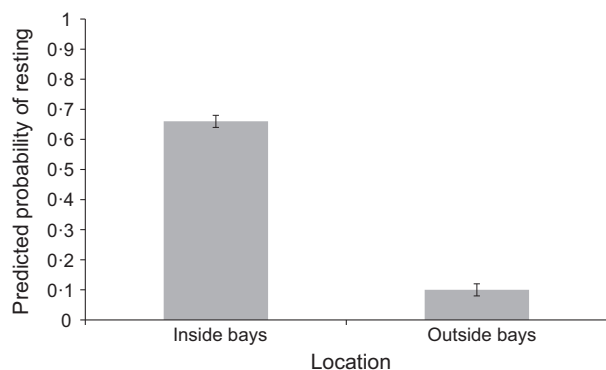


Fig. 2. Marginal function estimate showing the probability of spinner dolphins resting inside and outside of the four sheltered bays (Kauhako Bay, Honaunau Bay, Kealakekua Bay and Makako Bay). Error bars indicate 95% confidence intervals.

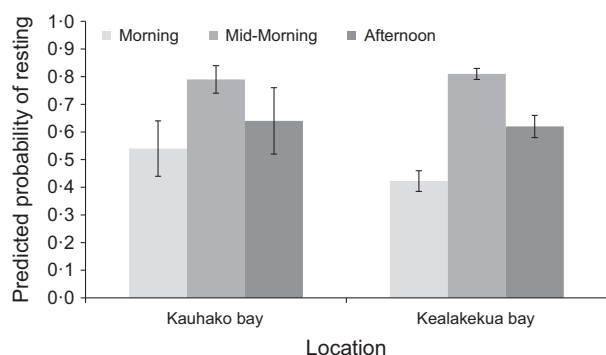


Fig. 3. Time-of-day (TOD) base-learner marginal function estimates showing the predicted probability of spinner dolphins resting ($\pm 95\%$ confidence intervals) during the morning (6 am–10 am), mid-morning (10 am–2 pm) and afternoon (2 pm–6 pm) for Kauhako Bay and Kealakekua Bay. Resting behaviour based on land-based observations.

ner dolphins (Norris *et al.* 1994; Thorne *et al.* 2012), by illustrating that dolphins are unlikely to rest outside of the key habitats that support this important life function. These results provide management agencies with information to assist in implementing an effective protected area management approach, to reduce the exposure of dolphins to human disturbance during resting periods.

Previous studies have shown that spinner dolphins rest over substrate types of low complexity within these bays, that is areas of sandy bottom, and usually in <60 m of water (Norris *et al.* 1994; Thorne *et al.* 2012). To date, however, studies evaluating spinner dolphin resting habitat have focussed only on areas inside bays. The results from this study show that some habitat variables (e.g. depth and distance from shore) were not important predictors of spinner dolphin rest. In fact, the most important factor contributing to the likelihood of rest was whether dolphins were within a bay or not. The interaction between substrate type and in-bay presence suggests that substrate (sand) is partially influential in predicting resting behaviour. In coastal areas outside of bays, spin-

ner dolphins spent disproportionately more time over sandy substrates than over other substrates available. However, in contrast to their behaviour in bays, dolphins seldom rested over these sandy substrates. Instead, they were observed mainly travelling over sand outside bays. This may be because the sandy substrate outside bays fails to provide spinner dolphins with as safe a place to rest than when inside bays (Norris *et al.* 1994).

Cetacean-based tourism has increased dramatically in Hawai'i over recent years (O'Connor *et al.* 2009) which has led to increased human exposure to spinner dolphins (Delfour 2007; Courbis & Timmel 2009). The cumulative exposure of dolphin populations to human interactions has had detrimental effects on bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau 2005), and on bottlenose dolphins, *Tursiops aduncus*, in Shark Bay, Western Australia (Bejder *et al.* 2006b; Higham & Bejder 2008). In New Zealand, resting has been identified as the most sensitive behavioural state to disturbance of one population of bottlenose dolphins (Lusseau 2004). Spinner dolphin resting behaviour is often interrupted or truncated by human activities, and they leave resting bays in direct response to human disturbance (Courbis & Timmel 2009). Rest is a vital component in the energy budgets of most animals (Cirelli & Tononi 2008); as animals tire, they become less vigilant and more vulnerable to predators (Dukas & Clark 1995). During night-time foraging bouts, spinner dolphins herd their prey to increase its density and then cooperatively feed on these high-density aggregations (Benoit-Bird & Au 2009). To recover from the energetically demanding foraging activity and increase their vigilance, spinner dolphins return to these sheltered bays to rest (Johnston 2014).

This study provides critical, but until now, missing evidence that outside sheltered bays, spinner dolphins are unlikely to rest. If dolphins leave resting bays to avoid disturbance from human activities, our results indicate that they are unlikely to rest and recover from the ongoing energetic and cognitive costs associated with their rigid daily schedules.

MANAGEMENT OF MARINE MAMMALS

The MMPA was originally designed to minimize the capture (or 'take'), harassment and disturbance of marine mammals, primarily from by-catch from fisheries and cetacean hunting. The MMPA defines the term 'take' as '... hunting, killing, capture and harassment of a marine mammal or the attempt thereof'. Harassment is defined as '... any act of pursuit, torment, or annoyance which (i) has the potential to injure a marine mammal or marine mammal stock in the wild; or (ii) has the potential to disturb a marine mammal or marine mammal stock in the wild by causing disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering.' Most human–dolphin interactions (boat-based or swim-with) cause behavioural

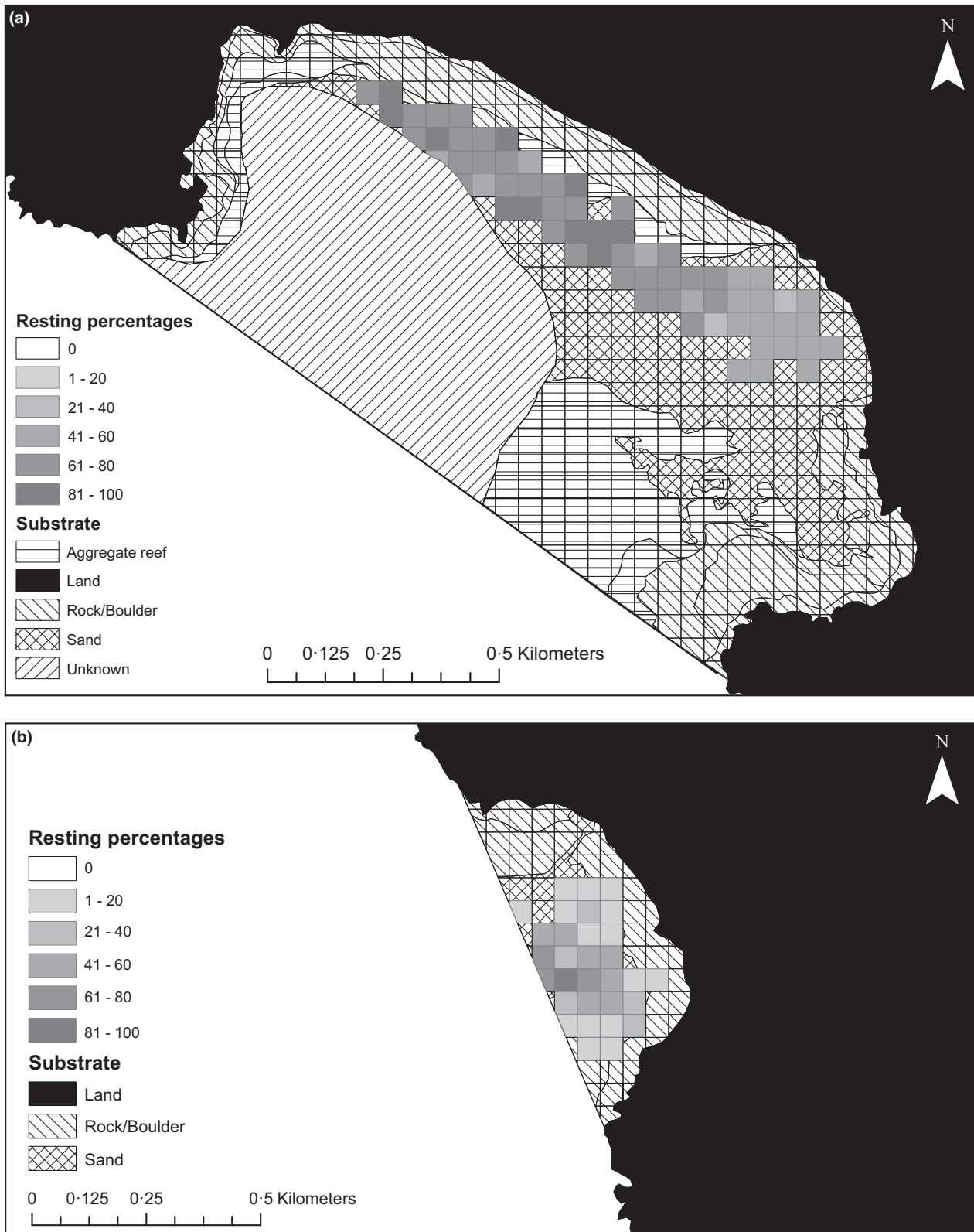


Fig. 4. Predicted percentages for resting spinner dolphins modelled from boosted generalized additive models in (a) Kealakekua Bay ($n = 1526$) and (b) Kauhako Bay ($n = 200$). Grid cells are 50 m² based on the resolution of available bathymetric and habitat maps.

disruptions in dolphins, which by the above definition is 'harassment'. The burden of proof in documenting dolphin behavioural changes as a consequence of human

activities rests with the management agency. However, interpreting dolphin behavioural changes as a consequence of human activities is challenging and often

clouded by arguments that any observed behavioural changes are a consequence of natural phenomena and not induced by human activity (Johnston 2014). This highlights a need for an enforcement policy to make legislation more easily understood, less ambiguous and more fairly enforced. In 2005, NOAA published an Advance Notice of Proposed Rulemaking about the concerns surrounding human–dolphin interactions, and to solicit feedback on potential options for future regulations under the MMPA (NOAA 2005).

MANAGEMENT IMPLICATIONS

The Hawai'i Island associated spinner dolphin population may be especially vulnerable to disturbance because it is small (Tyne *et al.* 2014), genetically isolated (Andrews *et al.* 2010) and is unlikely to rest outside sheltered bays. Humans often seek close-up interactions with spinner dolphins both inside and outside of important resting areas (Courbis & Timmel 2009; Wiener, Needham & Wilkinson 2009). Cumulative exposure to human interactions within resting habitats may be detrimental to spinner dolphins. Energetic models of spinner dolphins in Hawaiian waters indicate that they are less likely to rest when swimmers approach within 150 m (J. Symons, J.A. Tyne, L. Bejder, D.W. Johnston & D. Lusseau, unpublished data). Although the current level of swim-with exposure in this region does not appear to contribute to energetic deficits in spinner dolphins, research indicates that any further increase in intensity is likely to drive these dolphins into an energetic debt (J. Symons, J.A. Tyne, L. Bejder, D.W. Johnston & D. Lusseau, unpublished data).

These results support management actions to reduce human access to preferred dolphin resting areas during important resting periods. Using environmental, spatial and temporal estimates of key habitats and guidance from energetic models (J. Symons, J.A. Tyne, L. Bejder, D.W. Johnston & D. Lusseau, unpublished data), we highlight two management approaches that could be considered. The following options to mitigate possible detrimental effects of human activity on spinner dolphins are based purely from a biological and conservation perspective. Other factors (e.g. cultural and subsistence) (Heenehan *et al.* 2014) also need to be considered. Management options include, but are not limited to the following:

1. Restricting all human activity throughout bays during dolphin rest periods.
2. Restricting human access to specific habitats (sandy bottom) within resting bays during important dolphin rest periods in combination with implementing a buffer zone, for example 150–300 m, around these particular habitats.

Distances over water are difficult to estimate (Kinzey & Gerrodette 2003). Therefore, we recommend that any management action implementing restrictions to geographical regions should include surface markers to delineate the restricted areas (e.g. U.S. Fish & Wildlife Service 2001).

These management options take into account the need for an easily enforceable policy by providing unambiguous solutions that can effectively protect the spinner dolphins from harassment within important resting areas. Importantly, when exploring measures to protect spinner dolphin resting habitat, decision-makers should note conclusions of a recent review of marine protected areas which highlighted that the effectiveness of protected areas are dependent on protecting an area of adequate size and on compliance and enforcement (Edgar *et al.* 2014).

Interactions between human activities and marine vertebrates are often negative, and the approach developed here, where models explicitly link behaviour with habitat characteristics to identify important habitats for protection, is much needed. This approach is applicable to ongoing conservation conflicts, but could also be a component of recovery plans for depleted species. Such models could anticipate and avoid future conflicts as animals recover from exploitation and reoccupy portions of their ranges. For example, female and young calf humpback whales (*Megaptera novaeangliae*) use Exmouth Gulf, Western Australia, as a resting area (Braithwaite, Meeuwig & Jenner 2012). Exmouth Gulf has been earmarked for possible future resource exploration and aquaculture development, and there is a pressing need to identify crucial resting habitats and transit corridors before development begins. This approach would also be useful for recovering species of pinnipeds, such as grey seals off the US East Coast (Wood *et al.* 2011), where combined assessments of breeding behaviour and colony habitat characteristics could anticipate where new breeding colonies may form and how these colonies may interact with coastal communities and other components of the marine ecosystem.

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Data accessibility

The data set used in this manuscript will be made available in the Dryad data repository: doi: 10.5061/dryad.f624r. (Tyne *et al.* 2015).

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Supporting Information

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

Fig. S1. The proportion of time spinner dolphins were observed resting, socializing and travelling over available known substrate inside bays.

Fig. S2. The proportion of time spinner dolphins were observed resting, socializing and travelling over available known substrate outside bays.

Table S1. Definitions of spinner dolphin group activities.

Table S2. Proportion of substrate types available to spinner dolphins inside and outside of bays within the study area.