

Whalewatching boats disrupt the foraging activities of Minke whales in Faxaflói bay, Iceland

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ABSTRACT

We compared Minke whale behaviour in the presence and absence of whalewatching boats in Faxaflói Bay, Iceland, a feeding ground for the North Atlantic population. Individual focal follows were conducted from land (control) and from commercial whalewatching boats (impact). Minke whale activity states were inferred from movement metric data (inter-breath interval and directness index) and Linear Mixed Effects (LME) models were used to investigate the effect of whalewatching boats on the activity state of Minke whales. We identified three distinct activity states: surface feeding (conspicuous events of feeding observed at the surface), foraging (long dives and sinuous movement) and travelling (short dives and straight movement).

The presence of boats influenced the interaction between dive interval and directness index. Minke whales avoided whalewatching boats by decreasing their inter-breath intervals (performing shorter dives) and decreasing their directness index (increasing circular movement). An increase in respiration rate in the presence of whalewatching boats could reflect an increase in metabolic rate caused by avoidance behaviour. This could lead to an increase in energy expenditure of Minke whale during interactions with whalewatching boats. In addition, the long and relatively sinuous dives observed during foraging behaviour were absent during interactions with whalewatching boats. This indicates that whalewatching boats disrupt the foraging behaviour of Minke whales. Foraging is a biologically important activity for Minke whales in the feeding grounds, as the energy acquired in the feeding ground will set the limit to the amount of energy available for reproduction and lactation in the breeding ground. Thus the foraging disruption observed in this study could be of biological importance.

INTRODUCTION

Marine tourism is a lucrative business, with net revenue exceeding that of all marine fisheries and aquaculture together (Honey & Krantz 2007; UNEP 2008; FAO 2009). Whalewatching is part of marine tourism, and has been growing rapidly around the world during the last decades (O'Connor et al. 2009). Even though whalewatching seems to be reaching its carrying capacity in some regions, it still shows rapid growth in other regions, especially in developing countries (Lusseau et al. In press). Providing a global revenue of more than 2 billion USD a year (O'Connor et al. 2009), the economic benefits generated from whalewatching has the potential to be substantial in developing countries where economic opportunities are otherwise very limited.

In Iceland, whalewatching was introduced in 1991 and has since been growing rapidly (O'Connor et al. 2009). In 2008 the total income from whalewatching was about 16700 USD. That year more than 114000 people went whalewatching, mainly in Skjálfandi bay in the north (36%) and Faxaflói bay in the south (51%) (O'Connor et al. 2009). In Faxaflói bay, whalewatching takes places mainly in the south-eastern part of the bay (Fig. 1). There are currently four whalewatching companies operating in Faxaflói bay from the harbour of Reykjavik, providing a total of six boats which vary in size from 13 to 34 meters. During the summer months each boat conducts on average three trips per day. The mean duration of a trip is about three hours, resulting in whalewatching boats being present in the bay during most of the daylight hours (09:00-20:00 hours).

The target species of the whalewatching activities in Faxaflói bay is the Minke whale (*Balaenoptera acutorostrata*). The Minke whale is a migratory species that spend the summers feeding in the high latitude productive waters of the North Atlantic, including Iceland. Breeding is believed to take place somewhere near the equatorial waters of the Atlantic during the winters months (Vikingsson & Heide-Jorgensen 2005). Minke whales are present in Icelandic waters between early May and late October every year. Aerial surveys conducted in Icelandic waters in 2001 gave an estimate of 43,633 Minke whales (95% CI: 30,148-63,149) in Icelandic waters, of which 7,678 (95% CI: 4,984-11,830) were located in Faxaflói bay (Borchers et al. 2009).

Whalewatching interactions can cause short-term behavioural effects on cetaceans (Bejder, Dawson & Harraway 1999; Allen & Read 2000; Nowacek, Wells & Solow 2001a; Williams et al. 2002a; Lusseau 2006; Christiansen et al. 2010). For odontocetes, these behavioural effects can lead to long-term negative effects on vital rates (Bejder 2005; Fortuna 2006), which in turn can lead to population effects (Lusseau, Slooten & Currey 2006b). For mysticetes, data is currently insufficient to assess potential long-term effects of whalewatching. However, since most mysticetes are capital breeders they are more likely to be severely affected by whalewatching interactions taking place in their feeding grounds (Stephens et al. 2009), as the foraging success there will set the limits to the amount of energy that can be transferred to their calves in the breeding grounds. Therefore, developing studies to investigate long-term effects of whalewatching on mysticetes are urgently needed (IWC 2006).

For management, it is important to understand how short-term behavioural effects caused by whalewatching activities translate into long-term population effects, which is of biological significance. In 2005, the U.S. National Research Council (NRC) committee presented a conceptual framework to structure future studies of the potential population-level effects of changes in behaviour of marine mammals, named Population Consequences of Acoustic Disturbance (PCAD) (NRC 2005). The PCAD framework has since then been further developed into a more formal model structure, which defines the mechanistic link between disturbances and their consequences (International Whaling Commission 2010). The concept of the PCAD framework is that the presence of a *Source* (i.e. whalewatching boat) will lead to Behavioural changes (i.e. respiration rate, movement) of the targeted animal which affects the animals Life functions (i.e. activity: energy acquisition, energy expenditure). These are linked to Vital rates (survival and reproduction), which ultimately can lead to Population Effects (population growth rate) through a series of transfer functions (NRC 2005).

As already seen, many studies has managed to inform the link between the source of the impact and behavioural changes, using a wide range of response variables, including speed, movement, diving behaviour, group formation and vocalisation (Au & Perryman 1982; Janik & Thompson 1996; Constantine & Baker 1997; Nowacek, Wells & Solow 2001a; Van Parijs & Corkeron 2001; Stensland & Berggren 2007). However, linking behavioural changes to life functions has proven to be a much more difficult endeavour, as interpretation of the response variables in terms of life functions is not always straight forward. A good response variable to use for this purpose is the activity state of the animals, as long as states are chosen based on their relative contribution to life functions (e.g. foraging is related to energy acquisition while travelling is not). By looking at the effects of whalewatching on the activity state of cetaceans, some studies have managed to link the source of disturbance to life functions directly (Lusseau 2004; Williams, Lusseau & Hammond 2006; Christiansen et al. 2010). However, this approach limits the study design to discrete time series, while behaviour is likely to be a continuous time

process. Further, assessing the activity state of animals in the field by visual observations is susceptible to observer bias, as the observer needs to process information from the surface behaviours of animal (e.g. surface rates, movement patterns and group cohesion) in real time. The reliability of the data is thus strongly related to the observer's experience and knowledge of the study species, the local population etc, which further limits the use of this method.

This study presents a relatively cheap and effective way of collecting basic behavioural data on Minke whale movement, by using a land-based station and commercial whalewatching boats. Instead of visually determining activity states in the field, activity states are inferred from movement metric data (e.g. inter-breath intervals and directness index), thus providing a much more objective way of assessing activity states. This limits the potential errors to measurement errors rather than observer errors. Since this approach requires a minimum knowledge of the species and population to be able to collect data, the method is readily accessible to a larger group of potential users. The effect of whalewatching boats on Minke whale activity states is estimated and linked into the PCAD framework, providing the functional links between the source of the impact, behavioural changes and life functions.

METHODS

Data collection

The behaviour of Minke whales and whalewatching boats were collected by continuous individual focal follows (Altmann 1974) in Faxaflói bay, Iceland, between June and September 2010. Focal animals were chosen randomly and if another animal was in close proximity of the focal animal, the follow was terminated to avoid measurement errors from sampling the wrong animal.

Control data of undisturbed whales were collected from a land-based research platform, a 27 meter tall lighthouse (64°04'56''N, 22°41'24''W) located in Garður on the northern tip of the Keflavík peninsula (Fig. 1). Land-based research platforms have the advantage of not causing any effects on the behaviour of the animals studied (Bejder & Samuels 2003), but have limited visual range. In Faxaflói bay, interactions between whalewatching boats and cetaceans take place far from land (Fig. 1), which made it impossible to collect impact data from same research platform. Instead commercial whalewatching boats were used to collect impact data. Even though this type of research platform is restricted to data only being collected in the presence of a disturbance (Bejder & Samuels 2003), this was not a major drawback since the control data could be collected from land. Using commercial whalewatching boats also give the advantage that photo-identification data of the targeted whales could be collected together with the behavioural data, from which the exposure rate of individual whales could be estimated. The combined use of a land-based research platform and commercial whalewatching boats provided an inexpensive way to collect large samples of both control and impact data.

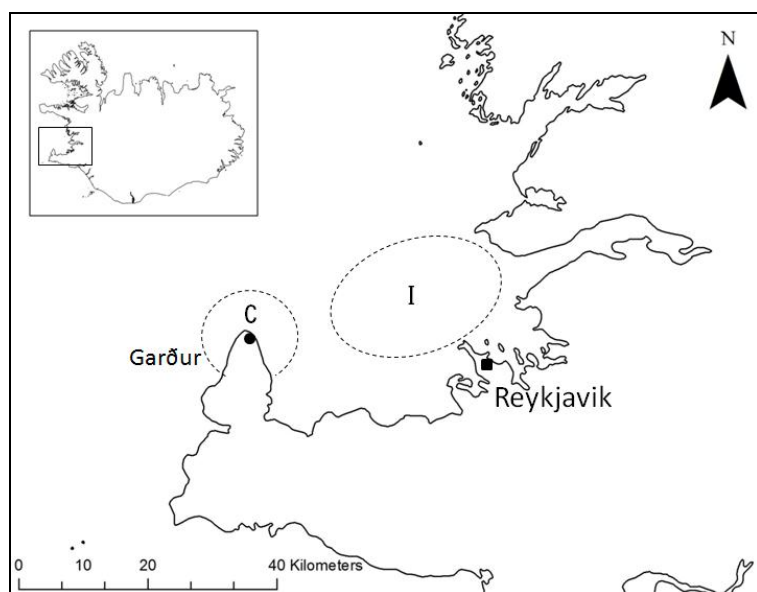


Fig. 1. Map of Faxaflói bay, Iceland. The areas inside the dashed lines correspond to the study area for the control (C) and impact site (I), respectively.

The time of every surfacing were recorded together with the true horizontal angle to the whale, as well as the vertical angle subtended between the horizon and the waterline of the whale. From land, both the horizontal and vertical angles were measured by using a theodolite (Wild T16). From the whalewatching boats, the horizontal angles were collected by a digital compass mounted on a range finder (LaserAce®300). The vertical angle subtended between the horizon and the waterline of the whale (θ), in radians, was derived from photographic images of every surfacing taken by an SLR camera (Nikon D80 with a Sigma 70-200mm lens) (Gordon 2001):

$$\tan(\theta) = \frac{(V/S)}{f \cdot C} \quad (1)$$

Where V is the distance between the horizon and the waterline of the whale on the photograph, in pixels, H is the picture height, in pixels, S is the height of the image sensor, in mm, f is the focal length of the camera lens, in mm, and C is the crop factor of the camera model. Measuring the range to animals at sea from boats by using photographic images gives a much higher accuracy compared to range estimation by eye or using reticule binoculars or laser range-finders (Gordon 2001). For each surfacing, the position of the research vessel was also recorded, using a handheld GPS unit (Garmin eTrex H).

The distance to the whale (D), in kilometres, were then calculated (Kinzey & Gerrodette 2003):

$$D = h_e * \sin(\theta + \alpha) - \sqrt{R_E^2 - (h_e * \cos(\theta + \alpha))^2} \quad (2)$$

Where θ is the vertical angle subtended between the horizon and the waterline of the whale, in radians, α is the angle above the horizon to the horizontal tangent, $\arctan\left(\frac{\sqrt{2R_E h + h^2}}{R_E}\right)$, in radians, h is the eye height of the observer above sea level (tidal level was accounted for in the land based data set), in kilometres, R_E is the radius of the earth (6371 km) and $h_e = R_E + h$ (Kinzey & Gerrodette 2003).

The latitudinal (Lat_w) and longitudinal ($Long_w$) positions (angles) of the whale, in radians, could then be calculated:

$$Lat_w = \arcsin\left(\sin(Lat_p) * \cos\left(\frac{D}{R_E}\right) + \cos(Lat_p) * \sin\left(\frac{D}{R_E}\right) * \cos(d)\right) \quad (3)$$

$$Long_w = Long_p + \arctan2\left(\cos\left(\frac{D}{R_E}\right) - \sin(Lat_p) * \sin(Lat_w); \sin(d) * \sin\left(\frac{D}{R_E}\right) * \cos(Lat_p)\right) \quad (4)$$

Where Lat_p and $Long_p$ is the latitudinal and longitudinal positions of the research platform (the observer), respectively, in radians, D is the distance between the observer and the whale (see equation 1), in kilometres, R_E is the radius of the earth (6371 kilometres) and d is the direction, or horizontal angle, to the whale, in radians. Arctan2 is in the format $\arctan2(x;y)$.

Surface conspicuous behaviours, such as surface feeding (engulfing manoeuvres), near-surface feeding (entrapment manoeuvres) and breaching were also recorded (Lynas & Sylvestre 1988), as was the presence of feeding birds near the whale, the total number of Minke whales in the area, as the presence of other cetacean species. Environmental factors, such as sea conditions (Beaufort scale), cloud cover and tidal height were also recorded.

Estimating movement metric variables

Minke whale inter-breath intervals (IBI), the time elapsed between two consecutive surfacing, were calculated from the surface times. If a surfacing time was missed, no IBI was calculated for that interval. Two movement metrics, deviation- and directness index, were calculated from the positional data and were used to describe the movement of Minke whales. The deviation index (DEV) is the relative turning angle between two adjacent dives, and is equivalent to the angle α in Fig. 2. The DEV for each surfacing in the track was calculated by estimating the angle between the direction of a dive (the direction between P_{t-1} and P_t in Fig.3) and the straight-

line direction predicted by the previous dive (the direction between P_{t-2} and P_{t-1} in Fig.3) (Williams, Trites & Bain 2002b). DEV ranges between 0° , straight movement, and 180° , erratic movement.

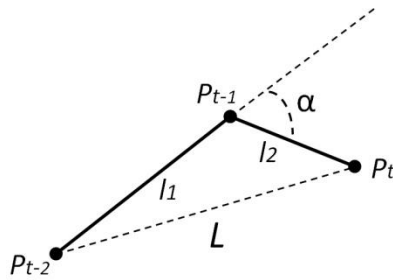


Fig. 2. Example of a movement track of a Minke whale with three surfacing (P_t , P_{t-1} and P_{t-2}) and two inter-breath intervals (IBI) (l_1 and l_2). The letter t denotes the temporal order of the surfacing with P_t being the present position, P_{t-1} the previous position and P_{t-2} the position of the whale two surfacing earlier. L is the distance between the end-points of the track. Angle α corresponds to the deviation index (DEV) for IBI $P_{t-1}-P_t$. The directness index (DI) for IBI $P_{t-1}-P_t$ is calculated by $DI=100(L/(l_1+l_2))$.

Directness index (DI), or the straightness of movement of each surfacing in the track, was calculated by dividing the distance between the end-points of the track, the distance between the present position and the position of the whale two surfacing earlier (L), by the actual distance of the track line, the sum of the distance between the present and previous position (l_2) and the previous position and its preceding surfacing (l_1) (Fig.2) (Williams, Trites & Bain 2002b). DI ranges between 0 (circular movement) and 100 (straight movement). Apart from the DI illustrated in Fig.2, a number of different versions of DI were calculated, based on three to six surfacing each, covering all possible combinations between a lag of one and three both before and after the present position of the whale (P_t).

Using movement metric data to infer activity states

To link the effect of whalewatching boats to life functions, the movement behaviour of Minke whales must first be linked to activity states. Thus, the first step is to identify the number of activity states of Minke whales in the feeding grounds and see which movement metrics best describes these. The activity states used in this study were Surface Feeding (SF), foraging (FOR) and travelling (TRA), which can be defined in terms of IBI, DEV and DI (table 1).

Table1. Definitions of Minke whale activity states in a feeding ground in terms of movement metrics and the associated life function of each state. IBI=Inter-breath interval, DEV=Deviation index, DI=Directness index.

Activity state	IBI	DEV	DI	Life functions	
				Energy acquisition	Energy expenditure
Surface feeding (SF)	Short	High	Low	Yes	Yes
Foraging (FOR)	Long	High	Low	Yes	Yes
Travelling (TRA)	Short	Low	High	No	Yes

Stomach content analysis of Minke whales caught in whaling operations show that sandeels (*Ammodytes sp.*) constitute the main part of the diet of Minke whales in Faxaflói bay (Gunnar Bergmann Jónsson, Minke Whale Association, pers. comm.). Sandeels have a patchy distribution and are relatively stationary in movement (Wright, Jensen & Tuck 2000). The surface feeding and foraging states of Minke whales should therefore be characterized by sinuous movement (high DEV and low DI), representing an animal staying within the same foraging patch, which corresponds well with the literature on foraging Minke whales (Hoelzel, Dorsey & Stern 1989; Macleod et al. 2004). Surface feeding whales should have relatively short IBI (Curnier 2005; Baumgartner 2008), as they are staying close to the surface during their foraging dives. However, whales foraging on prey further below the surface should have relatively longer IBI during their foraging dive (Folkow & Blix 1992; Curnier 2005), to maximize the rate of energy acquisition. In contrast, the behaviour of travelling Minke whales

is defined by relatively straight movement (low DEV and high DI) and relatively short IBI (Folkow & Blix 1992; Curnier 2005).

To relate activity states to life functions, the contribution of each state to bioenergetics needs to be defined. The two main components of bioenergetics in energy expenditure, for maintaining body metabolism, growth, reproduction and daily behaviour, and energy acquisition from prey consumption (IWC 2008). The activity state that relates to energy acquisition is thus surface feeding and foraging, while all three activity states have certain energy expenditure. Because Minke whales are capital breeders, reproduction is absent from the activity state repertoire of Minke whales whilst in their feeding grounds.

Measuring whalewatching effects on activity states

Linear Mixed Effect (LME) models were used in R 2.12 (R Development Core Team 2010) to investigate at the effects of whalewatching boats on the activity state of Minke whales. To find out if activity states could be inferred from the movement metric data, IBI was modelled as a function of DEV and DI separately. Apart from linear relationships, different polynomial relationships between the dependent and independent variables were tested. The presence of surface feeding behaviours was added as a categorical variable. The effects of whalewatching boats on Minke whale activity states were then investigated by adding the presence of whalewatching boats as a fixed covariate. In the model selection process, covariates and interactions between covariates were added sequentially to the null model based on biological explanation and the F-statistic for the ANOVA F-test was estimated for each model and compared to the previous model.

Since the data was compiled of several observations within the same follows, observations within follows could not be considered independent from each other. To account for this, a temporal auto-correlation structure was incorporated in the model, where the residuals at any given time are modelled as a function of the residuals of the previous time points. Follow number was used as a grouping factor so that the auto-correlation structure was applied only to observation within the same follow, while different follows were assumed to be uncorrelated. The most suitable auto-correlation structure was fitted by altering the number of auto-regressive (AR) and moving average (MA) parameters and then comparing the different models. Auto-Correlation Function (ACF) and Partial Auto-Correlation Function plots were used to visually detect patterns of AR and MA before and after adding the different correlation structures.

To further improve model fit, different random effects were added to the model, to help explain some of the residual variance. Different variance structures were also added to improve model fit and to account for any potential variance heterogeneity. Restricted Maximum Likelihood estimation (REML) was used for estimating the model parameters. The best fitting model was selected using Akaike's Information Criterion (AIC).

Dealing with error propagation

Data collected by GPS, theodolite, range finder and from photographs (the pixel count) all come with their own intrinsic or extrinsic measurement errors. To account for error propagation in the model, the error for each measurement tool was first estimated by making repeated measurements of the same object, from which the standard deviation of the measurements was calculated. Measurement errors were assumed to be normally distributed. The model was then bootstrapped 1000 times, with values for each itinerary being taken randomly from a distribution of values, which mean's corresponded to the originally measured values and the standard deviation's being the one's obtained from the repeated measurement tests. The bootstrapping process generated a density distribution around the estimate of each model parameter, as well as their associated standard errors.

RESULTS

Sample size

Data was collected on 67 days between the 29th of May and 28th of August 2010, giving a total of 88 hours of Minke whale observations. A total of 5574 surfacing were recorded from 545 follows, from which 4943 IBI could be calculated. The position of 3578 surfacing (679 control, 2899 impact) were recorded, from which 2486 estimates of DEV and DI were obtained (444 control, 2042 impact). From the impact data, 131 data points (6.4%) were excluded as the vertical angle subtended between the horizon and the waterline of the whale (θ) were not visible in the photographs, or were obscured by a nearby land mass. Similarly, 25 control data points (5.6%) were excluded from the analysis because of observer bias. The effective sample size after the data sorting process was 2330 data points (419 control, 1911 impact) belonging to 293 follows (53 control, 240 impact), which gives an average of eight data points (SD=7.87) per follow.

Model selection and validation

During the model selection process, model validation tests were run to identify potential violations of the underlying assumptions of the models. The response variable, IBI, needed to be log transformed not to violate the model assumption of homogenous variances, after failing to account for this by incorporating different variance structures in the model. Table 2 shows the results of the LME model.

Table 2. Results of model selection using LME models. IBI=Inter-breath interval, DI=Directness index, Boat=Vessel presence, SF=Surface feeding, Follow=Follow number, AR=Auto-regression.

Model	Correlation structure	Random effect	Variance structure	df (among)	df (within)	AIC	ΔAIC
log(ISI)~DI*Boat*SF				8	2322	6260	145
log(ISI)~DI*Boat				4	2326	6237	122
log(ISI)~DI*Boat	~Follow (AR=1)			4	2326	6209	94
log(ISI)~DI*Boat	~Follow (AR=1)	~Follow		4	2326	6165	50
log(ISI)~DI*Boat	~Follow (AR=1)	~Follow	σ^2_{Boat}	4	2326	6145	30
log(ISI)~(DI+DI ²)*Boat	~Follow (AR=1)	~Follow	σ^2_{Boat}	4	2326	6115	0

The movement metric that best described the IBI of Minke whales were DI. Based on the AIC values, the best fitting version of DI was the one based on the present and previous two positions of the whale (as presented in Fig. 2). The polynomial model tests revealed a quadratic polynomial linear relationship between the log(IBI) and DI (Table 2). While DI ($F_{2,2033}=2.802$, p-value=0.0609) and vessel presence ($F_{1,291}=0.129$, p-value=<0.7193) alone didn't have a significant effect on Minke whale IBI, the interaction between the two variables was significant ($F_{2,2033}=3.971$, p-value=<0.0190). This suggests that the effect of whalewatching boats on Minke whale IBI is depending on the DI, and hence activity state, of the animal. Surface feeding activity could not be distinguished from the other activity states based on movement metrics alone, and adding surface feeding as a variable (SF) did not improve the fit of the model (Table 2). The ACF and PACF diagnostic plots showed a clear violation of the independence assumption, with a significant residual correlation of lag one. This indicates that the length of an IBI of a Minke whale at any given time is dependent on the previous IBI. By adding a temporal auto-correlation structure of AR=1, the model fit improved greatly (Table 2), as did the ACF and PACF plots. By adding follow number as a random effect in the model, 0.048 of the variance could be explained, which further improved the model fit (Table 2). The residual variance, σ^2 , was estimated as 1.054. The relatively small variance for the random effect means that there is a small difference in IBI between Minke whales, in terms of the intercept. Homogeneity of variances was assessed by plotting the standardized residuals against fitted values of the model, which showed no signs of heteroscedasticity. Residuals were also plotted against each explanatory variable used in the model. The variance structure showed slightly different standard deviations between the control and impact data, with the later containing 83% of the variation observed in the control data. This indicates a greater variation in diving behaviour of Minke whales in the absence of whalewatching boats, with Minke whales being more constrained in IBI in the presence of whalewatching boats, even after taking the fixed effects into account. The heterogeneity in variance between the control and impact data was incorporated in the model by fitting a variance structure with different variances per stratum (j) for vessel presence, $\varepsilon_{ij} \sim N(0, \sigma_j^2)$, which further improved the model fit (Table 2). Normality of residuals was verified from Quantile-Quantile plots as well as histograms of the residuals. The model was also assessed for influential observations and outliers by using Cook's distance and leverage, respectively, but showed no extreme values. Because r-square values can not be obtained from LME models, this is not presented here.

The effects of whalewatching on activity states

The diving pattern of Minke whales in the absence of whalewatching boats is generally a series of short dives followed by a longer dive (Fig. 3). These long dives occurs both during foraging and travelling behaviour (Fig. 3) and can thus not be used alone as a variable to tell the two activity states apart. However, since foraging is defined by sinuous movement (low DI), longer dives occurring within this range of DI are most likely representing foraging dives, as represented by the top left rectangle in Fig. 3. Travelling on the other hand, is represented by straight movement (high DI, Fig. 3). Surface feeding is defined by relatively short dives, which also occurs during sinuous movement, corresponding to the rectangle in the lower left corner of Fig. 3. However, when looking at the distribution of surface feeding observations, surface feeding becomes impossible to separate from travelling based on movement metric data alone (Fig. 3).

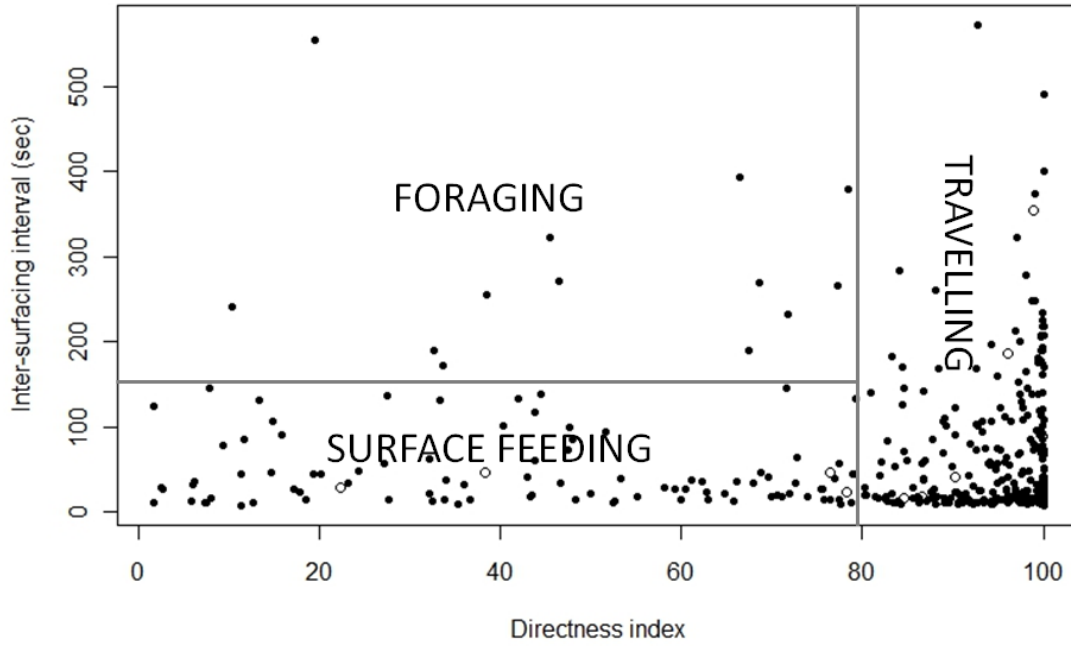


Fig. 3. Inter-breath intervals (IBI) of Minke whales as a function of directness index (DI) in the absence of whalewatching boats (control). The three rectangles represent the expected distribution of the different activity states. The open circles represent observed surface feeding (SF) events.

The fitted control data show a clear increase in IBI with lower DI values, indicating the presence of foraging dives in the absence of whalewatching boats (Fig. 4). In contrast, the impact data show a decrease in IBI at lower DI values. This indicates that foraging dives are absent during interactions with whalewatching boats (Fig. 4).

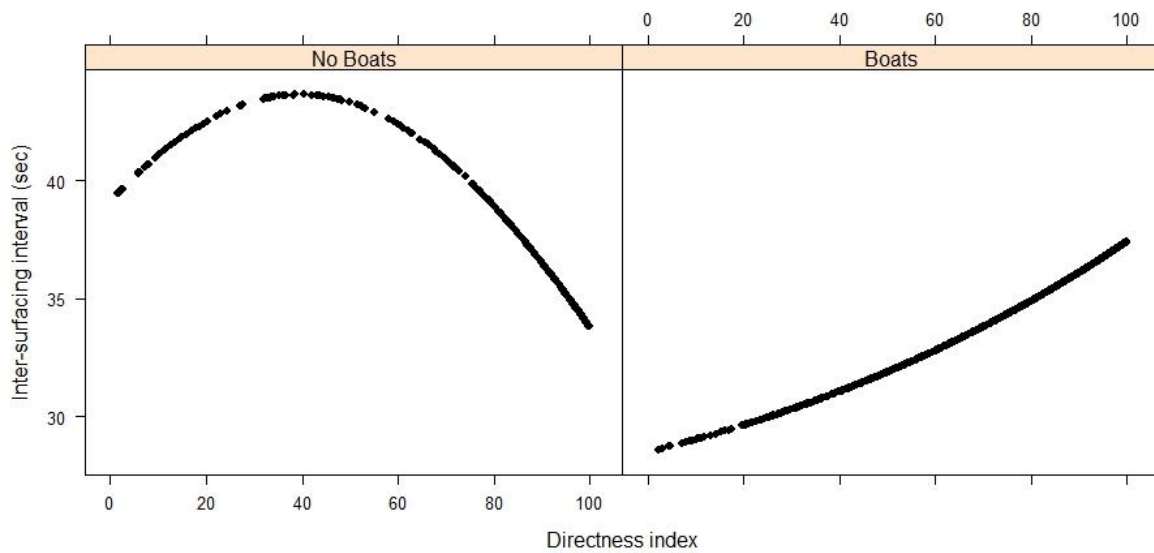


Fig. 4. Back-transformed fitted values of inter-breath interval (IBI) as a function of directness index (DI) in the absence and presence of whalewatching boats.

Effects of error propagation

Parameter values were relatively narrow in their distribution, indicating that measurement errors had little effect on parameter estimates (Fig. 5). The standard errors for the parameter estimates were all normally distributed and did not cross zero, again indicating minor effects from measurement errors (Fig. 5). Measurement errors also had a negligible effect on the variance estimate of the random effect (follow) as well as the residual variance estimate of the best fitting model (Fig. 6).

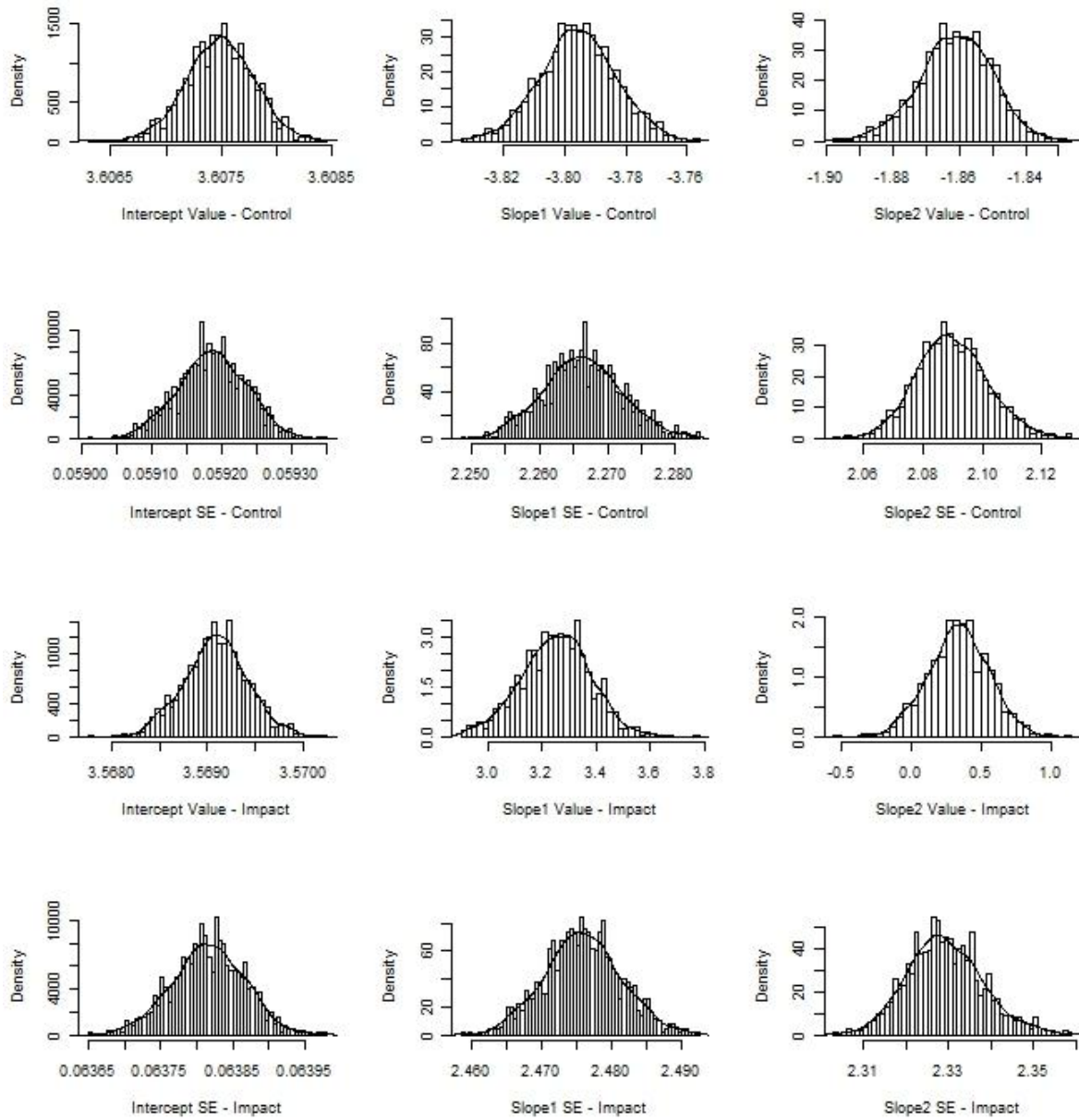


Fig. 5. Density distributions of the parameter values (Value) and their associated standard errors (SE) for the best fitting model.

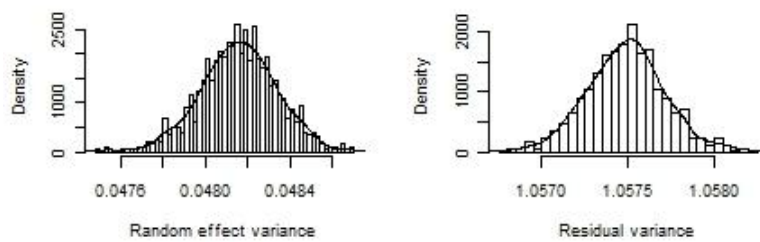


Fig. 6. Density distributions of the random effect and residual variance for the best fitting model.

DISCUSSION

Using movement metric data to infer activity states

This study shows that movement metric data can be used to infer activity states of Minke whales in the wild. By modelling IBI as a function of DI, it was possible to differentiate between foraging and travelling activities (Fig. 3). Even though surface feeding activity could not be differentiated from foraging and travelling by movement metrics alone, the fact that it's a conspicuous behaviour makes it possible to differentiate surface feeding from other activity states based on this visual cue. Surface feeding can thus be defined by a categorical variable (presence of surface feeding events) while foraging and travelling can be defined by combining two continuous variables (IBI and DI).

The method described in this paper provides a simple, but robust way of collecting unbiased behavioural data of Minke whales. Since activity is inferred from movement metric data, rather than being estimated by an observer directly, bias due to observer subjectivity is avoided. The method requires a minimum knowledge of cetaceans, and can therefore be used by most whalewatching operators to gather data to assess the potential impact of their business on cetaceans. Since movement metric data can be collected opportunistically from commercial whalewatching boats, or from land-based research platforms, this study provides a relatively inexpensive way to collect valuable data for impact assessment studies (Bejder & Samuels 2003). The LaWE proposal of the IWC highlights the need of developing a standardized modelling framework, including the minimum set of variables needed, to predict the potential population effects of whalewatching activities on cetaceans (IWC 2010). For solitary cetacean species, such as the Minke whale and most other mysticetes, the methods used in this study could provide such a framework, and be further developed to suit all species of cetaceans.

The within follow auto-correlation structure used in this model made it possible to collect several measurements of IBI and DI from the same follow, without violating the model assumption of independence. This approach allowed a much more detailed measurement of Minke whale diving behaviour than simply using the mean value for each movement metric for the entire follow (Williams, Trites & Bain 2002b). Since a single follow can include several activity states within it, a simple mean will not be able to capture the dynamics of diving behaviour within follows, and will lead to a loss of biologically important information.

Evaluating the effects of whalewatching on Minke whales in Faxaflói Bay

Minke whales in Faxaflói bay responded to whalewatching boats by decreasing their IBI and increasing sinuous movements (decreasing DI). Similar responses have been observed in other studies of cetaceans, including mysticetes, with whalewatching activities causing either an increase (Nowacek, Wells & Solow 2001a; Lusseau 2003; Schaffar et al. 2009) or decrease (Stone et al. 1992) in IBI. An increase in respiration rate in the presence of whalewatching boats could reflect an increase in metabolic rate caused by higher energy demand during avoidance behaviour. Minke whales thus need to surface more frequently in the presence of whalewatching boats to maintain an adequate oxygen supply. Horizontal avoidance is another strategy used by cetaceans to avoid whalewatching boats (Williams et al. 2002a), by increasing the frequency of heading changes to outmanoeuvre or confuse the “predator”. This could explain the increase in sinuous movement of Minke whales during interactions with whalewatching boats.

The relationship between IBI and DI was markedly different between control and impact situations (Fig. 4). The long and relatively sinuous dives observed during foraging behaviour were absent during interactions with whalewatching boats. This indicates that whalewatching boats disrupt the foraging behaviour of Minke whales. Further, the impact data actually show a decrease in IBI at lower values of DI, even below the values normally observed during travelling (Fig. 4). The lower values of IBI at lower DI (sinuous movement) is most likely defining the avoidance behaviour of Minke whales towards whalewatching boats, resulting from an increase in metabolic rate and an increase in erratic movement.

That whalewatching boats are disrupting the behaviour of Minke whales in Faxaflói bay is further indicated by the observed difference in variance structure between the control and impact data, with the later containing 83% of the variation observed in the control data. This means that Minke whales show a greater variation in IBI in the absence of whalewatching boats, likely reflecting a greater degree of plasticity in diving behaviour. The decrease in variance observed during impact situations, suggest that the diving behaviour of Minke whales becomes restrained during interactions with whalewatching boats, possibly as an effect of animals trying to avoid interactions by pushing themselves closer to their physiological limits.

That Minke whales show anti-predator responses towards whalewatching boats means that the animal perceives whalewatching boats as predation risk (Frid & Dill 2002). The perceived predation risk is influenced by a number of factors related to the disturbance stimuli (Beale & Monaghan 2004a), the targeted individual (Beale & Monaghan 2004b), the social structure of the species (Frid & Dill 2002), and the environment (Heithaus & Dill

2006). From a management perspective, altering the factors related to the disturbance stimuli (i.e. whalewatching boats) is the most direct approach to minimizing the perceived predation risk, and thus the effect of whalewatching boats on Minke whales. Future studies should therefore aim to identify which factors related to the whalewatching activities (e.g. number of boats, distance, speed etc) is the main drivers behind the avoidance behaviour, and focus management actions towards minimizing these effects. In the absence of such data, whalewatching should be considered as a black box (assuming that all interactions have the same effect) and exposure caps (limit of acceptable change) should be set to prevent potential long-term population effects.

Individual are likely to differ in their response to whalewatching boats, due to individual differences in age- (Constantine 2001), sex- (Lusseau 2003b), reproductive class (Nowacek, Wells & Solow 2001a), physiological condition (Beale & Monaghan 2004b) and temperament (Réale et al. 2007) and that animals play different roles in their populations (Lusseau unpublished data). Even though most of these factors are likely to influence the effect of whalewatching boats on Minke whales in Faxaflói bay, neither could be included in the analysis, as we were unable to record this data in the field. Individual variations in diving behaviour were instead accounted for by including follow as a random effect in the LME model, thus absorbing some of the variance attributed to individual variations in IBI. The low variance given by the random effect, follow, means that the difference in IBI between individual Minke whales was relatively low. We plan on further developing photogrammetric techniques to inform this follow variability.

Informing the PCAD model

The goal of this study was to inform the first links of the PCAD framework, between the source of the impact (whalewatching boats), behavioural changes (IBI and DI) and life functions (energetics) (NRC 2005). The first link was described in the sections above. By first inferring activity states from behavioural data, as shown in this study, the second link of the PCAD framework can then be informed by quantifying the relationship between the different activity states and bioenergetics (energy acquisition and energy expenditure).

Energy expenditure can be estimated from Minke whale respiration rates (Folkow & Blix 1992; Williams & Noren 2009). Since the effect of whalewatching boats were measured on movement metrics, rather than on activity states (Christiansen et al. 2010), this allows us to model energy expenditure on a continuous scale directly from the IBI, which provides much more accurate estimates of energy expenditure, than using discrete values of IBI for each activity state. This highlights another benefit of using movement metric data to infer activity states quantitatively.

Estimating the cost of whalewatching interactions on energy acquisition is more challenging. The link between foraging time and energy acquisition can potentially be estimated by direct measurements of prey consumption, by using an echo sounder (Benoit-Bird & Whitlow 2003) or be derived indirectly from studies of stomach content (Vikingsson 1997) or from inter seasonal trends in energy storage (blubber thickness) (Vikingsson 1990; Vikingsson 1995). If those are lacking, it can also, more vaguely, be informed by basic predation functional response types.

Being a capital breeder, Minke whales are likely to be severely affected by whalewatching boats disrupting foraging activity in their feeding grounds (Stephens et al. 2009), as the energy acquired in the feeding ground will set the limit to the amount of energy available for reproduction and lactation in the breeding ground. A decrease in foraging success due to whalewatching boats could therefore lead to a decrease in calf survival, which could have long-term population effects. The foraging disruption observed in this study could therefore be of biological importance.

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