

Whale watching disrupts feeding activities of minke whales on a feeding ground

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ABSTRACT: Human disturbances of wildlife, such as tourism, can alter the activities of targeted individuals. Repeated behavioural disruptions can have long-term consequences for individual vital rates (survival and reproduction). To manage these sub-lethal impacts, we need to understand how activity disruptions can influence bioenergetics and ultimately individual vital rates. Empirical studies of the mechanistic links between whale-watching boat exposure and behavioural variation and vital rates are currently lacking for baleen whales (mysticetes). We compared minke whale *Balaenoptera acutorostrata* behaviour on a feeding ground in the presence and absence of whale-watching boats. Effects on activity states were inferred from changes in movement metric data as well as the occurrence of surface feeding events. Linear mixed effects models and generalised estimation equations were used to investigate the effect of whale-watching boat interactions. Measurement errors were quantified, and their effects on model parameter estimates were investigated using resampling methods. Minke whales responded to whale-watching boats by performing shorter dives and increased sinuous movement. A reduction in the probability of observing longer inter-breath intervals during sinuous movement showed that whale-watching boat interactions reduced foraging activity. Further, the probability of observing surface feeding events also decreased during interactions with whale-watching boats. This indicates that whale-watching boats disrupted the feeding activities of minke whales. Since minke whales are capital breeders, a decrease in feeding success on the feeding grounds due to whale-watching boats could lead to a decrease in energy available for foetus development and nursing on the breeding grounds. Such impact could therefore alter the calving success of this species.

KEY WORDS: Tourism impact · Behavioural disruption · Animal movement · Error propagation · Cetacean

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INTRODUCTION

The frequency of human–wildlife interactions is increasing globally as a consequence of growing human populations. Besides the classical lethal interactions with wildlife (e.g. hunting), management of non-lethal interactions becomes increasingly important. At the centre of this emerging concern are human recreational activities in which people seek to interact with animals (Duffus & Dearden 1990). Even though such interactions are non-lethal, repeated behavioural disturbances caused by these human activ-

ities can have long-term consequences for the targeted wildlife populations (Lusseau et al. 2006). Whale watching is a lucrative business (e.g. nearly 13 million people went whale watching in 119 countries in 2008), generating 2.1 billion USD in total revenues (O'Connor et al. 2009). Whale-watching activities have been increasing rapidly around the world during the last few decades so that now most coastal cetacean populations are exposed to some form of whale watching (O'Connor et al. 2009). Whale-watching interactions can cause short-term behavioural effects on cetaceans (Nowacek et al. 2001,

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Williams et al. 2002, Lusseau 2003, Schaffar et al. 2009, Christiansen et al. 2010). For toothed whales (odontocetes), cumulative effects caused by repeated disturbance can lead to long-term negative effects on individual vital rates (survival and reproduction) (Bejder 2005, Fortuna 2006), which can have population-level consequences (Lusseau et al. 2006, Currey et al. 2009). Data to assess potential long-term effects of whale watching on baleen whales (mysticetes) are currently lacking. From the available impact studies, we understand that cetaceans perceive whale-watching interactions as a risk and adjust their behaviour accordingly depending on the behavioural ecology of the population and the species life-history strategy (Frid & Dill 2002, Beale & Monaghan 2004, Wirsing et al. 2008). Repeated exposure to disturbance risks placing the targeted animals under energetic constraints. Human-induced behavioural changes can have 2 associated costs: increased energy expenditure and/or decreased energy acquisition (Williams et al. 2006). In the latter case, the costs associated with lost foraging opportunities might be a lot higher than those caused by increased energy demands resulting from avoidance behaviour (e.g. increased swimming speed) (Williams et al. 2006). Bioenergetic consequences resulting from behavioural changes can affect the body condition of animals, and consequently have long-term negative effects on individual vital rates (NRC 2005). Cetaceans are *K*-selective species, so negative effects on vital rates are most likely to express themselves as negative effects on reproduction and calf survival, rather than affecting adult survival (Costa 2007, Stephens et al. 2009).

To what extent behavioural changes might affect individual vital rates depends on the animals' life-history strategy, as well as ecological constraints. For example, if the population's ecological landscape does not provide opportunity for recovery (time or habitat for resting) or compensation (e.g. feeding at night), behavioural disturbances are more likely to lead to impact on vital rates (Lusseau et al. 2008). Similarly, some species have evolved behavioural strategies in which individuals are trying to maximise energy acquisition over a short period (maximising food intake on feeding grounds) or minimise energy expenditure (conserve energy for lactation on breeding grounds). In this regard, capital and income breeders will vary in their sensitivity and ability to cope with human disturbance (Costa 2007, Stephens et al. 2009).

Most mysticete species are considered capital breeders because they have feeding and reproduc-

tion segregated in time (Costa 1993). They spend a prolonged period in high-latitude productive waters to develop energy reserves during summer, which they can then invest in calf rearing at low latitude during winter. The feeding success on the feeding grounds will limit the amount of energy that can be transferred to their calves on the breeding grounds (Costa 1993). A decrease in feeding success caused by repeated disruption of feeding activity is likely to have negative effects on maternal condition at parturition, which will have negative effects on nursing and calf survival (vital rates) (D. Lusseau et al. unpubl. data). Hence, whale-watching disturbance on the feeding grounds can have significant negative effects on individual vital rates.

In Faxaflói Bay, Iceland, minke whales *Balaenoptera acutorostrata* have been the main target of a fast-growing whale-watching industry (O'Connor et al. 2009). Minke whale is a migratory species that spends 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 winter months (Vikingsson & Heide-Jørgensen 2005). An estimated 43 633 minke whales (95% CI: 30 148 to 63 149 whales) were in Icelandic waters in 2001, of which 7678 (95% CI: 4984 to 11 830 whales) were located in Faxaflói Bay (Borchers et al. 2009). Minke whales are mainly present in Icelandic waters between mid-April and mid-October; however, they have been sighted all year round in Faxaflói Bay by whale-watching operators. Our objective in the present study was to investigate the effects of whale watching on the feeding activity of mysticetes on a feeding ground using minke whales in Faxaflói Bay as a study system.

MATERIALS AND METHODS

Behavioural sampling protocol

The behaviour of minke whales and whale-watching boats was recorded by continuous individual focal follows (Altmann 1974) in Faxaflói Bay, Iceland (Fig. 1) between June and September 2010 and 2011. 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. Minke whales tend to be solitary animals and this therefore happened rarely. In Faxaflói Bay, whale watching takes place mainly in the southeastern part of the bay (Fig. 1).

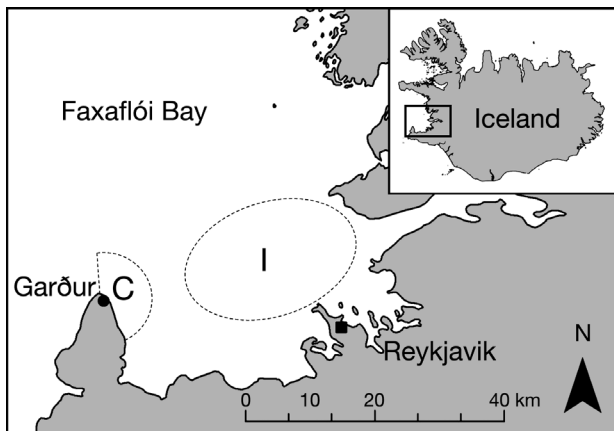


Fig. 1. Faxaflói Bay, Iceland. Areas inside the dashed lines correspond to the study area for the control (C) and impact sites (I)

There are currently 4 whale-watching companies operating in Faxaflói Bay from Reykjavik, with 6 boats varying in size from 13 to 34 m. During the summer months, each boat conducts on average 3 trips per day. The mean duration of a trip is about 3 h, resulting in whale-watching boats being present in the bay during most day hours (09:00 to 20:00 h).

Control data were collected from a 27 m tall lighthouse (64° 04' 56" N, 22° 41' 24" W) located in Garður on the northern tip of the Reykjanes peninsula (Fig. 1). Behavioural data was only collected from whales located within Faxaflói Bay (corresponding to the eastern side of the lighthouse; Fig. 1), as the habitat of this area is most similar to that of the whale-watching area, to avoid any confounding effects of environmental heterogeneity. In Faxaflói Bay, interactions between whale-watching boats and cetaceans take place far from land (>10 km), which made it impossible to collect impact data from the same research platform. Instead, impact data were collected from commercial whale-watching boats. The combined use of a land-based research platform and commercial whale-watching boats provided an inexpensive way to collect large sample sizes of both control and impact data.

The impact data collected from the whale-watching boats were all considered interactions between minke whales and whale-watching boats, irrespective of boat distance from the whale, numbers of boats and other factors (e.g. the speed of the boat, vessel type, the angle of approach to the whales, and noise level of the engine). Although our visual observations were limited to a distance of about 3000 m, studies on both odontocetes and mysticetes show that cetaceans can respond to boats at distances up to sev-

eral kilometres away (Au & Perryman 1982, Richardson et al. 1985). Although it is likely that the distance to the boat (as well as other factors relating to the whale-watching boats) could influence the behaviour of the whales, the aim of the present study was to assess whether there was a general effect of whale-watching boat presence on minke whale behaviour, not to quantify how the different covariates associated with the interaction influence this effect.

Data collection (observations)

An overview of the approach used to evaluate the effects of whale watching on minke whale activity states, and how the different parts of the methods section are linked together, can be seen in Fig. 2. Every time a whale surfaced to breathe, the time was recorded instantaneously. The position of the whale at every surfacing was also recorded by measuring the true horizontal angle to the whale, as well as the vertical angle subtended between the horizon and the waterline of the whale (θ). From land, the horizontal and vertical angles were measured using a theodolite (Wild T16, Wild Heerbrugg). From the whale-watching boats, the horizontal angle was collected with a digital compass mounted on a laser

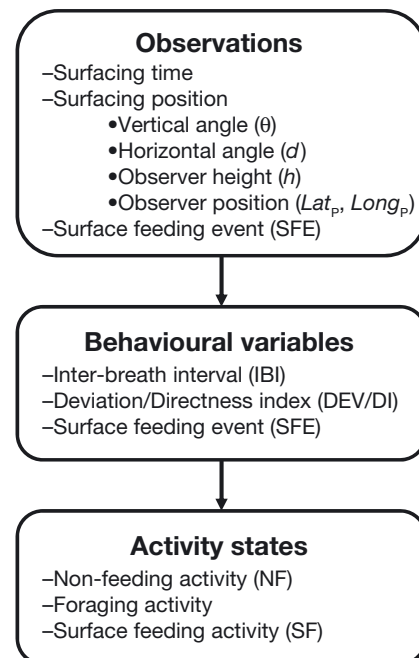


Fig. 2. *Balaenoptera acutorostrata*. Conceptual diagram showing how behavioural observations are linked to behavioural variables, which in turn are used to infer whale-watching effects on minke whale activity states

range finder (LaserAce® 300, MDL). The vertical angle θ was derived from photographic images of every surfacing taken with an SLR camera (Nikon D80 with a Sigma 70–200 mm lens) (Gordon 2001):

$$\tan(\theta) = \frac{\left(\frac{V}{H} \times S\right)}{f \times C} \quad (1)$$

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 of the camera, 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 distance to animals at sea from boats by using photographic images gives a much higher accuracy compared to distance estimation by eye or using reticle 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, Garmin).

The distance to the whale (D , in km) was then calculated following Kinzey & Gerrodette (2003):

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

where θ is in radians; α is the angle above the horizon to the horizontal tangent, $\arctan(\sqrt{2R_E h + h^2} / R_E)$ in radians; h is the eye height of the observer above sea level, in km; R_E is the radius of the earth (6371 km); and $h_e = R_E + h$ (Kinzey & Gerrodette 2003). The height of the land-based platform was corrected for tidal influence, estimated from measured tidal data from Reykjavik harbour at 10 min intervals.

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

$$Lat_W = \arcsin\left(\sin(Lat_P) \times \cos\left(\frac{D}{R_E}\right) + \cos(Lat_P) \times \sin\left(\frac{D}{R_E}\right) \times \cos(d)\right) \quad (3)$$

$$Long_W = Long_P + \arctan2\left(\cos\left(\frac{D}{R_E}\right) - \sin(Lat_P) \times \sin(Lat_W); \sin(d) \times \sin\left(\frac{D}{R_E}\right) \times \cos(Lat_P)\right) \quad (4)$$

where Lat_P and $Long_P$ are the latitudinal and longitudinal positions of the research platform (the observer), respectively, in radians; and d is the direction, or horizontal angle, to the whale, in radians. Arctan2 is the 2-argument arctangent.

Surface feeding events (SFE; direct observations of minke whales engulfing prey at the surface) (Lynas & Sylvestre 1988) were also recorded during focal follows. The occurrence of SFE was used as a categori-

cal variable, with SFE being either present or absent during a surfacing.

Environmental factors, such as sea conditions (Beaufort scale, visually estimated) and tidal height (data provided by the Icelandic Maritime Administration), were also recorded.

Accounting for measurement biases

The positional data of the whales were estimated from measurements collected by various instruments (GPS, theodolite, range finder and photogrammetry), each with its own intrinsic measurement errors (instrument precision). When several measurements are used together to calculate variables, the individual errors can propagate in the model. If sufficiently large, these errors can ultimately affect the outcome of the analysis by either masking the effect of whale watching or result in false detections of effects. A potential difference in measurement biases between the land-based (control) and boat-based sampling (impact) could result in a false detection of a difference between the control and impact data incorrectly assumed to be caused by whale-watching boats. To account for such potential measurement biases, individual measurement errors for each measurement tool (instrument) were estimated and corrected for when estimating the positional data. For the land-based (control) data, theodolite measurement errors were measured by taking repeated measurements of an object of known position (i.e. research boat) at various distances from the land-based research platform. The relationship between the measured (theodolite) distance and the true distance (GPS) were investigated using linear models in R (R v2.12 2011). Correction factors were added to the distance estimation formula (Eq. 2) until a perfect positive correlation between measured and true distance were obtained (intercept = 0, slope = 1). The errors in distance estimates (theodolite distance minus GPS distance) as a function of true distance (GPS) were estimated and correction factors added until the errors were homogeneously distributed around zero (intercept = 0, slope = 0). The same approach was used to estimate the errors in bearing estimates (theodolite bearing minus GPS bearing), as a function of distance. For the boat (impact) data, the same method as for land was used to estimate the errors in distance (photogrammetry distance minus GPS distance) and bearing (range finder bearing minus GPS bearing) estimates as a function of distance, by taking repeated measurements of an object of known position (i.e. another whale-watching boat).

Estimating movement metrics (behavioural variables)

From the surfacing times, minke whale inter-breath intervals (IBI) were estimated as the time elapsed between 2 consecutive surfacings. If a surfacing time was missed, no IBI was calculated for that interval. Potential biases resulting from observer errors (individual variation and experience level) on the probability of missing a surfacing were tested for (Supplement 1 at www.int-res.com/articles/suppl/m478p239_supp.pdf). Deviation and directness indices were calculated from the corrected positional data (Fig. 3) and were used to describe the movement of minke whales (Williams et al. 2002). The deviation index (DEV) is the relative turning angle between 2 adjacent dives (α in Fig. 3). 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 et al. 2002). DEV ranges between 0° (linear movement) and 180° (erratic movement). Directness index (DI), or the linearity of movement of each surfacing in the track, was calculated by dividing the distance between the end-points of the specific section of the track (L , the distance between the present position and the position of the whale two surfacings earlier), by the actual distance of the track line of the section (the sum of the distance between the present and previous position, l_2 , and the previous position and its preceding surfacing, l_1) (Fig. 3) (Williams et al. 2002). DI ranges between 0, circular movement, and 100, linear movement. Apart from the DI illustrated in Fig. 3, a number of different versions of DI were

calculated, based on 3 to 6 surfacings each, covering all possible combinations between a lag of 1 and 3 both before and after the present position of the whale (P_t).

Linking movement metrics to activity states

To infer the effect of whale-watching boats on minke whale activity, the movement behaviour of minke whales must first be linked to activity states. In terms of bioenergetics, the activity of an animal can broadly be divided into feeding and non-feeding (NF) activities, the former being related to energy-acquiring activities and the latter, energy-expending activities. For minke whales, feeding activity can either be directly observed at the surface or take place deeper down in the water column (Lynas & Sylvestre 1988). We will refer to these 2 forms of feeding as surface feeding (SF) and foraging, respectively. The 3 activity states used in the present study were defined from IBI, DEV and DI movement metrics (Curnier 2005, Bailey & Thompson 2006, Stelle et al. 2008, Bailey et al. 2009), as well as observation of SFE (Lynas & Sylvestre 1988, Bertulli 2010) (Table 1).

Stomach content analyses of minke whales show that sandeel *Ammodytes* sp. is predominant in their diet in Faxaflói Bay (Vikingsson & Elvarsson 2010). Sandeels have a patchy distribution and are relatively stationary in movement (Wright et al. 2000). The SF and foraging states of minke whales should therefore be characterised by sinuous movement (high DEV and low DI), representing an animal staying within the same foraging patch (Hoelzel et al. 1989, Bailey & Thompson 2006, Stelle et al. 2008). SF whales should have relatively short IBI (Curnier

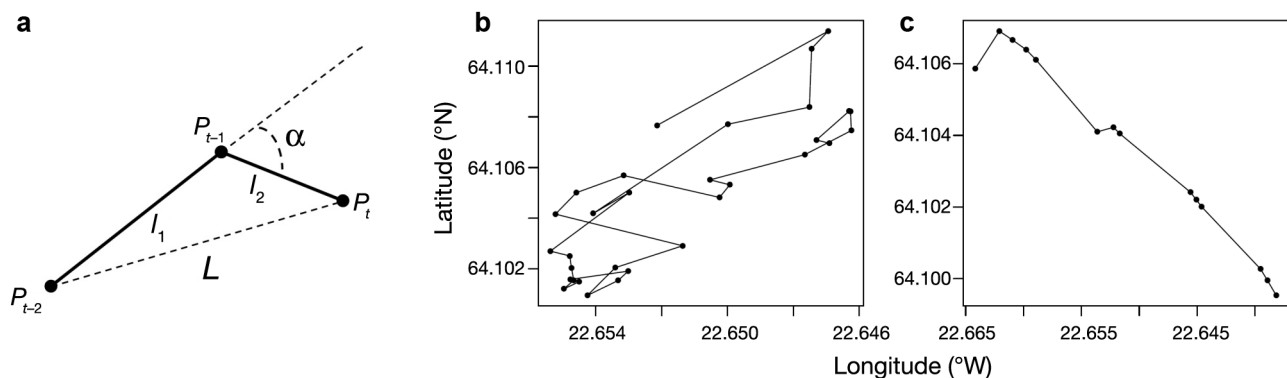


Fig. 3. *Balaenoptera acutorostrata*. (a) Example of a movement track of a minke whale with 3 surfacings (P_t , P_{t-1} and P_{t-2}) and 2 inter-breath intervals (IBI) (l_1 and l_2); P_t is the present position, P_{t-1} the previous position, etc. and L is the net distance travelled between P_t and P_{t-2} . The deviation index for l_2 is α . The directness index (DI) for l_2 is calculated by $DI = 100 \cdot [L / (l_1 + l_2)]$. Example of minke whale movement tracks during (b) foraging and (c) non-feeding activity

Table 1. *Balaenoptera acutorostrata*. Definitions of minke whale activity states on a feeding ground in terms of movement metrics and the associated bioenergetic function (energy acquisition or expenditure) of each state. DEV = deviation index, DI = directness index, IBI = inter-breath interval, SFE = surface feeding event. Sources—a: Lynas & Sylvestre (1988), b: Bertulli (2010), c: Curnier (2005), d: Bailey & Thompson (2006), e: Bailey et al. (2009), f: Stelle et al. (2008)

Activity state	DI low and DEV high		DI high and DEV low		SFE	Bioenergetic functions		Source
	IBI short	IBI long	IBI short	IBI long		E. acquisition	E. expenditure	
Surface feeding (SF)	✓	–	–	–	✓	✓	✓	a, b
Foraging	–	✓	–	–	–	✓	✓	c, d, e, f
Non-feeding (NF)	✓	–	✓	✓	–	–	✓	c, d, e, f

2005), as they are staying close to the surface during their dives and display SFE. Whales foraging on prey below the surface should have relatively longer IBI during their foraging dives (Folkow & Blix 1992, Curnier 2005) to maximise prey intake. All other combinations of IBI and horizontal movement metrics (DEV or DI) should represent NF activity (Table 1). NF activity therefore includes not only shorter and longer IBI occurring during linear movement (low DEV and high DI) (Bailey et al. 2009), often referred to as ‘travelling’ in other studies (Stelle et al. 2008), but also shorter IBI occurring during sinuous movement (high DEV and low DI), which could represent preparatory dives occurring just before a foraging or SF dive. While preparatory dives surely serve another purpose than the ordinary NF dives, there is no difference in terms of bioenergetics (Table 1). To be able to differentiate between these preparatory dives and SF activity, the latter was also defined by the presence of SFE.

Measuring whale-watching effects on movement metrics

The effects of whale-watching boats on minke whales’ activity states were inferred from changes in movement metric data, which we investigated using generalised least squares (GLS) and linear mixed effects (LME) models (nlme package; Pinheiro et al. 2011). IBI was first modelled as a function of DEV and DI separately to find out which horizontal movement metric best described the observed variance in IBI of minke whales. Prior observations (described in the previous section ‘Linking movement metrics to activity states’) implied that non-linear relationships between these variables may exist. We therefore fitted polynomial relationships between the dependent and independent variables and tested whether they explained better the observed variability than linear relationships did. The presence of SFE was added as

a categorical variable. The effects of whale-watching boats on minke whale movement metrics were then investigated by adding the presence of whale-watching boats as a fixed covariate influencing the relationship between IBI and DEV or DI. In the model selection process, covariates and interactions between covariates were added sequentially to the null model, and the *F*-statistic for the ANOVA *F*-test was estimated for each model and compared to the previous model. The variance inflation factor (VIF) was used to investigate collinearity (high correlation) between the explanatory variables in the model (car package; Fox & Weisberg 2011). A threshold value of 3 was used to remove collinear variables one at a time until all VIF values were below 3 and no collinearity remained.

Observations within follows could not be considered independent from each other. To account for this, a temporal auto-correlation structure within follows was incorporated in the model, where the residuals at any given time were modelled as a function of the residuals of the previous time points. The most suitable auto-correlation structure was fitted by altering the number of auto-regressive and moving average parameters and then comparing the different models. Auto-correlation function and partial auto-correlation function plots were used to visually detect patterns of auto-regressive and moving average parameters before and after adding the different correlation structures.

We could expect variance heterogeneity to arise in these models because whale-watching interactions might restrict the diving behaviour of minke whales, which would result in less variation in IBI during impact situations. Hence, we tested whether adding variance structures that described these mechanisms improved model fit. Restricted maximum likelihood estimation was used for estimating the model parameters. The overall best-fitting model was selected using Akaike’s information criterion (AIC) and the Bayesian information criterion (BIC).

We also assessed the effect of whale-watching boat presence on SF activity, by estimating the probability of observing SFE, using generalised estimation equations (GEE) (geepack package; Halekoh et al. 2006). Models included a dependence structure for an overdispersed binomial model with a logit link function, which can account for within-follow dependence (temporal or spatial) between observations.

Although the positional data used to estimate horizontal movement metrics were corrected for measurement biases, each measured position still came with a level of uncertainty, resulting from measurement errors. In order to assess the sensitivity of our results to this error heterogeneity, we propagated sampling errors in fitted models using Monte Carlo approaches (Supplement 1).

RESULTS

Data were collected on 118 days during 2 field seasons between June and September 2010 and 2011, giving a total of 164 h of minke whale observations. A total of 11 873 surfacings were recorded from 1358 follows, from which 10 276 IBI could be calculated (Table 2). The position of 8793 surfacings (2757 control, 6036 impact) were recorded, from which 5978 estimates of DEV and DI were obtained (1659 control, 4319 impact). From the impact data, 396 data points (9.2%) were excluded, as θ was not visible in the photographs, or was obscured by a nearby land mass. The effective sample size after data censoring was 5582 data points (1659 control, 3923 impact) belonging to 797 follows (279 control, 518 impact; mean: 7 data points [SE = 0.28] per follow).

The duration of minke whale follows in the absence of whale-watching boats varied between <1 and 99 min (mean: 7.97 ± 10.53 min), while interac-

tion time between whale-watching boats and minke whales varied between <1 and 62 min (8.50 ± 8.54 min). The distance between a vessel and a whale ranged between 20 and 2600 m (402.80 ± 227.95 m). The number of boats during interactions varied between 1 and 5 (1.47 ± 0.69).

Accounting for measurement biases

For the land-based (control) data, 184 theodolite measurements were taken of a known object (research boat), across a range of distances between 2500 and 6000 m. By adding a correction factor of +17.689 for the intercept and $\times 1.039$ for the slope, a near-perfect positive correlation between measured (theodolite) and true (GPS) distances was obtained ($SE_{\text{intercept}} = 9.91$, $SE_{\text{slope}} = 0.003$). The coefficient of determination of the linear model showed that the accuracy of the theodolite measurements, in terms of measuring true distances, was very high ($R^2 = 0.99$). Adding the correction factors also made the distance measurement errors homogeneously distributed across distances. For bearing, a small correction factor of -0.901 for the intercept was needed ($SE_{\text{intercept}} = 0.025$, $SE_{\text{slope}} < 0.001$), which is reasonable considering that a bearing is a true value and not relative, so adding a correction factor for the slope parameter would not be logical. Once again, the coefficient of determination showed a very high accuracy for theodolite bearing measurements ($R^2 = 1.00$), with the bearing measurement errors being homogeneously distributed across distances.

For the boat-based (impact) data, distances were measured from 61 photographs of a known object (whale-watching boat) at distances between 80 and 900 m. Correction factors of +10.691 for intercept and $\times 1.25$ for slope were needed to obtain a near-perfect positive correlation between measured (photogrammetry) and true (GPS) distances ($SE_{\text{intercept}} = 2.82$, $SE_{\text{slope}} = 0.006$). The coefficient of determination of the linear model showed that the accuracy of the photographic measurements was very high ($R^2 = 0.99$). The correction factors made the distance measurement errors homogeneously distributed across distances. For bearing, 48 measurements of true bearing were recorded between 130 and 1800 m with the range finder. A correction factor of -16.38 was needed for the intercept to reach zero ($SE_{\text{intercept}} = 1.63$, $SE_{\text{slope}} = 0.003$), which gave a high coefficient of determination for the model ($R^2 = 0.99$), as well as homogeneously distributed bearing measurement errors across distances.

Table 2. Movement metric data of minke whales in Faxaflói Bay, Iceland, with (impact) or without (control) whale-watching boats present. IBI = inter-breath interval, DEV = deviation index, DI = directness index; n = number of valid observations

		Mean \pm SD	Min	Max	n
IBI (s)	Control	68 \pm 86.56	2	703	3506
	Impact	52 \pm 58.12	3	608	6770
DEV (°)	Control	70 \pm 60.28	0	180	1710
	Impact	71 \pm 51.62	0	180	4040
DI	Control	84 \pm 24.96	0.7	100	1725
	Impact	82 \pm 22.07	3.1	100	3983

Table 3. *Balaenoptera acutorostrata*. Selection of models explaining the observed variance in log-transformed inter-breath interval. GLS = generalised least squares, LME = linear mixed effects, DEV = deviation index, DI = directness index, Boat = vessel presence, SFE = surface feeding event, Follow = follow number, AR = auto-regression, AIC = Akaike's information criterion, BIC = Bayesian information criterion

Model no.	Model type	Fixed effects	Correlation structure	Variance structure	Random effects	df (among)	df (within)	AIC	BIC	Δ AIC	Δ BIC
1	GLS	Boat				2	5566	14981	15001	279	226
2	GLS	DEV				2	5566	15005	15024	302	249
3	GLS	DI				2	5566	14999	15019	297	244
4	GLS	DI + Boat				3	5565	14993	15019	291	244
5	GLS	DI \times Boat				4	5564	14970	15003	268	228
6	GLS	DI \times Boat + SFE				5	5563	14975	15014	273	239
7	GLS	DI \times Boat + Year				5	5563	14935	14975	233	200
8	GLS	DI \times Boat \times Year				8	5560	14963	15023	261	248
9	GLS	DI \times Boat + Year	~Follow (AR = 1)			5	5563	14907	14953	205	178
10	GLS	DI \times Boat + Year	~Follow (AR = 1)	σ^2_{Boat}		5	5563	14862	14915	159	139
11	LME	DI \times Boat + Year	~Follow (AR = 1)	σ^2_{Boat}	~Follow	5	5563	14747	14807	45	32
12	LME	(DI + DI ²) \times Boat + Year	~Follow (AR = 1)	σ^2_{Boat}	~Follow	7	5561	14702	14775	0	0

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 was log-transformed to meet the homoscedasticity assumption.

The horizontal movement metric that best described the variance in IBI of minke whales was DI (Model 3 in Table 3). Collinearity between DEV and DI ($VIF_{\text{DEV}} = 3.46$, $VIF_{\text{DI}} = 3.46$) prevented the use of both variables in the model. The best-fitting version of DI was the one based on the present and previous 2 positions of the whale. The polynomial model tests revealed a quadratic polynomial linear relationship between $\log(\text{IBI})$ and DI (Model 12 in Table 3). DI ($F_{2,4781} = 4.76$, $p = 0.0086$) and vessel presence ($F_{1,794} = 12.15$, $p = 0.0005$) both had a significant effect on minke whale IBI. In addition, the interaction between the 2 variables was significant ($F_{2,4781} = 18.74$, $p < 0.0001$), suggesting that the effect of whale-watching boats on minke whale IBI depended on DI, and hence on the activity state of the animal. IBI also varied between years ($F_{1,794} = 26.31$, $p < 0.0001$), which could not be accounted for by observer effects (year effect when censoring the data to keep only 1 observer: $F_{1,379} = 21.58$, $p < 0.0001$). The best-fitting model also included auto-correlation of IBI within follows, variance attributed to a random effect of focal follows ($\sigma^2_{\text{follow}} = 0.056$, $\sigma^2_{\text{residuals}} = 0.945$) and variance heterogeneity between treatment levels (vessel presence) ($\epsilon_{ij} \sim N(0, \sigma_{ij}^2)$) (Model 12 in Table 3). The relatively small variance for the random effect meant that there was a

small difference in IBI between minke whale follows. Variance heterogeneity indicated a greater variation in diving behaviour of minke whales in the absence of whale-watching boats, and minke whales being more constrained in IBI in the presence of whale-watching boats, even after taking the fixed effects into account. Similar effects were observed when considering DEV instead of DI (Supplement 2 at www.int-res.com/articles/suppl/m478p239_supp.pdf).

Effects of whale watching on activity states

The diving pattern of minke whales in the absence of whale-watching boats is generally a series of short dives followed by a longer dive. When looking at a density distribution of $\log(\text{IBI})$, the 2 dive types become apparent as 2 distinct peaks, the first lower peak (left peak in Fig. 4a) representing long dives and the second higher peak (right peak in Fig. 4a) representing short dives. In the absence of boats, these long dives occurred throughout the range of DI values (Fig. 4a). Thus, IBI could not be used as a variable alone to distinguish between foraging and NF activity. However, since foraging activity was defined by sinuous movement (low DI), long dives occurring within the lower range of DI were most likely representing foraging activity, whereas long dives occurring within the higher range of DI (linear movement) most likely belonged to NF activity.

The fitted control data showed a quadratic relationship between IBI and DI (Fig. 5a). During linear movement (high DI), IBI was relatively low, but started to

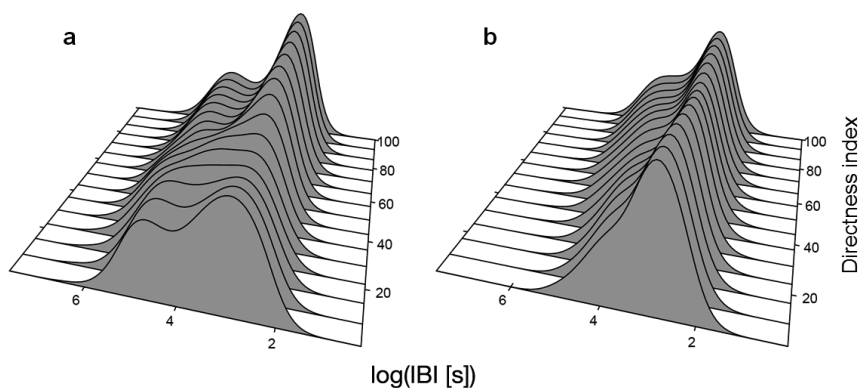


Fig. 4. *Balaenoptera acutorostrata*. Conditional density plots (hdrdce package; Hyndman et al. 1996) showing log-transformed inter-breath interval (IBM) of minke whales as a function of directness index in the (a) absence (control; $n = 1659$) and (b) presence (impact; $n = 3923$) of whale-watching boats. Note direction of x-axes (high to low)

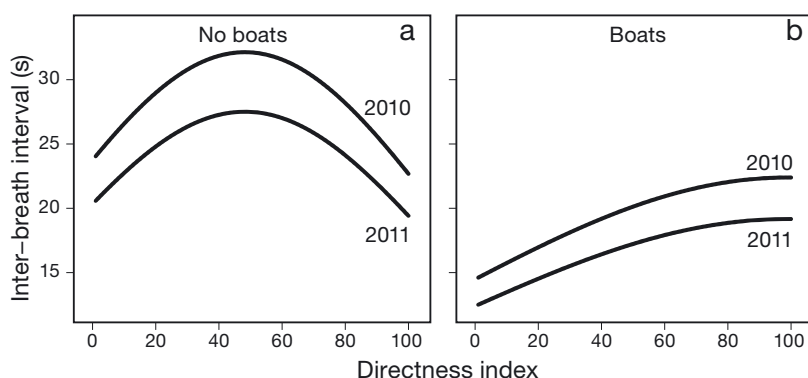


Fig. 5. *Balaenoptera acutorostrata*. Back-transformed fitted values of inter-breath interval from the best model (Model 12 in Table 3) as a function of directness index in the (a) absence (control; $n = 1659$) and (b) presence (impact; $n = 3923$) of whale-watching boats during 2010 and 2011

increase when movement became more sinuous and DI values decreased, indicating the presence of foraging dives in the absence of whale-watching boats (Fig. 5a). This increase in relative frequency of long dives during sinuous movement (low DI) was also visible in the density distribution of $\log(\text{IBM})$, as an increase in the relative height of the first peak (Fig. 4a), indicating the presence of foraging activity. In contrast, the impact data showed a decrease in IBM at lower DI values (Fig. 5b). This indicated that the relative frequency of foraging dives decreased during interactions with whale-watching boats. This effect was visible in the density distribution of $\log(\text{IBM})$, as a gradual reduction of the first peak towards the lower range of DI values, representing a decrease in foraging activity (Fig. 4b). Sensitivity analyses showed that the results were robust to measurement errors associated with the sampling techniques used to estimate the position of whales at the 2 field sites (Fig. 6).

SF activity could not be distinguished from the other activity states based on movement metrics alone, and adding SFE as a variable did not improve the fit of the model (Model 6 in Table 3). This justified the use of a separate GEE model to measure the effect of whale-watching boats on SF activity. Whale-watching boats had a significant effect on the probability of observing SFE ($\chi^2_1 = 16.4$, $p < 0.0001$), with whales being less than half as likely to perform SFE in the presence of whale-watching boats (probability of 0.018, 95% CI = 0.0148 to 0.0220, compared to probability of 0.040, 95% CI = 0.0349 to 0.0466). The correlation between 2 sequential observations within the same follow (the estimated correlation parameter) in the model was 0.14 (SE = 0.086).

DISCUSSION

Effects of whale watching on minke whales in Faxaflói Bay

This study is one of only a few studies investigating the effects of whale watching on the activity of mysticetes. The whales responded to whale-watching boats by decreasing their IBM and increasing sinuous movements (decreasing DI). Similar responses have been observed in other studies of cetaceans, including mysticetes, with whale-watching activities causing either an increase (Nowacek et al. 2001, Lusseau 2003, Schaffar et al. 2009) or decrease (Stone et al. 1992) in IBM. However, previous studies could not elucidate the consequences of this change in behaviour for activity because the IBM variable was used in isolation from information about the whales' horizontal movement. The relationship between IBM and DI was markedly different between control and impact situations (Figs. 4 & 5). The reduction in probability of observing longer IBM during sinuous movement (lower DI) showed that whale-watching boat interactions reduced foraging activity of minke whales. Further, the impact data actually show a decrease in IBM at lower values of DI, even below the values normally observed during NF activity (Fig. 5b). The lower values of IBM at lower DI (sinuous movement) are most

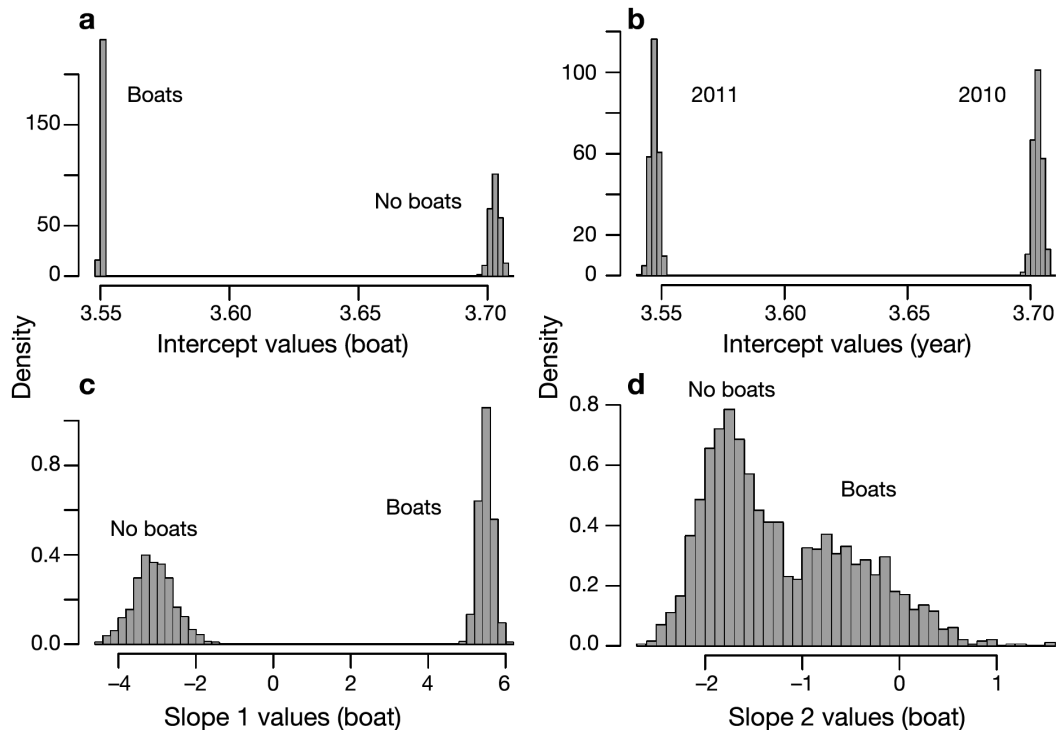


Fig. 6. Density distributions of parameter values (a) intercept values (boat), (b) intercept values (year), (c) Slope 1 values (boat), and (d) Slope 2 values (boat), for the best-fitting model (Model 12 in Table 3) based on 1000 bootstrapping iterations. All parameter values were relatively narrow in their distributions, indicating that measurement errors had little effect on parameter values. There was no overlap between (a) intercept values and (c) Slope 1 values, in the presence and absence of boats, as well as between (b) years, demonstrating that results were robust to measurement errors

likely defining the avoidance behaviour of minke whales towards whale-watching boats, resulting from an increase in metabolic rate and an increase in erratic movement. Even though SF activity could not be captured by using movement metrics (IBI and DI), a separate analysis showed that SF activity (defined from the observation of SFE) were less likely to occur in the presence of whale-watching boats. This further supports the hypothesis that whale-watching boats disrupt the feeding activities (foraging and SF) of minke whales in Faxaflói Bay. In addition, the observed IBI variance in the impact treatment was more constrained than in the control treatment. This means that minke whales show a greater variation in IBI in the absence of whale-watching boats, likely reflecting a greater variability in diving behaviour. The decrease in variance observed during impact situations suggests that the diving behaviour of minke whales becomes constrained during interactions with whale-watching boats. Possibly, animals are pushed closer to their physiological limits when trying to avoid boat interactions. In support of this, F. Christiansen et al. (unpubl.) found that minke whales increased swimming speed during interactions with whale-watching boats, which resulted in an increase

in metabolic rate and consequently respiration rate (decrease in IBI).

In 2011, minke whales had a significantly lower IBI than in 2010 (Fig. 5). The year effect could be due to different ecological conditions between years, which could have influenced the surfacing behaviour of minke whales (Lusseau et al. 2008). The fact that the effect of whale-watching boats was the same between years, however, could indicate that the behavioural response of minke whales to whale-watching boats is independent of ecological conditions. Further, there was no spatial difference in ecological conditions between the control and impact areas (McLeish 2012), so the measured difference in minke whale behaviour between areas was likely due to whale-watching activity.

As capital breeders, the reproductive success of minke whales could be strongly affected by disrupted feeding activities on the feeding grounds (Stephens et al. 2009). The magnitude of this effect will vary depending on the ability of the animal to compensate for a loss in energy acquisition at another time, which will be determined by the plasticity in feeding activity. Energetic data from minke whales in Iceland show a linear increase in blubber volume throughout

the feeding season (Christiansen et al. 2013). Hence, individuals are trying to maximise their energy intake throughout the season in order to build up energy reserves for breeding. Any lost feeding opportunity will therefore affect the total amount of reserve a whale can acquire during the summer season (Costa 1993). This behavioural strategy (i.e. capital breeding) therefore offers little opportunity for the whales to compensate for these losses. This low plasticity in behaviour, caused by the animals' life history, could help explain the low variance associated with the individual (follow) random effect. This suggests that minke whales are biologically constrained by their physiological target to maximize energy acquisition while on the feeding grounds. The feeding disruptions observed in the present study could therefore be of biological importance.

Further, mark-recapture photo-identification data indicate that some individual minke whales show relatively strong site fidelity to Faxaflói Bay and the whale-watching area (Bertulli 2010). This means that minke whales are most likely subject to numerous repeated exposures to whale-watching boats throughout the feeding season, which could result in cumulative effects on feeding success. Future research should aim to estimate this exposure rate to quantify the cumulative effects of whale watching on minke whales in Iceland.

Observational sampling of movement metric data to measure whale-watching effects

The present study demonstrates how multiple research platforms with different intrinsic measurement biases can be used together in impact assessments. We show that by quantifying these individual measurement biases, it is possible to correct for them before evaluating the effect of whale-watching boat interactions. Consequently, this allowed us to conclude that the measured difference between the control and impact data was really due to whale-watching boats, and not merely the result of a difference in measurement biases between the 2 research platforms. Resampling methods further showed that the model results were robust to measurement errors (Fig. 6). The method described in the present paper thus provides a simple, but robust way of collecting unbiased behavioural data of solitary cetacean species from multiple research platforms. Since movement metric data can be collected opportunistically from commercial whale-watching boats or from land-based research platforms, this study provides a rela-

tively inexpensive way to collect data for impact assessment studies. Further, recordings of surfacing times and positions can be made without much prior knowledge of the study species, and therefore make the method useful for studies of species for which little information exist.

While our modelling approach makes it possible to identify effects of whale-watching boats on minke whale activity states, it does not quantify these effects in terms of time allocation pattern (activity budget), which would provide a more direct link to bioenergetics (NRC 2005). The next step is therefore to quantitatively identify and classify individual dives into different activity states to estimate the effect of whale-watching boat interactions on the activity budget of animals. The present study shows that such a classification is possible for minke whales, by using movement metric data to distinguish between foraging and NF activity, and the presence of SFE to classify SF activity.

Management implications

From a management perspective, there is little need to regulate whale watching unless the measured behavioural disruptions are likely to lead to biologically significant population-level effects. The only way to evaluate these effects is to understand the mechanistic link between behavioural change and vital rates. The present study provides the mechanistic link between the source of the impact, behavioural changes and bioenergetics for mysticetes. Energy expenditure can be estimated from minke whale respiration rates (Folkow & Blix 1992, Williams & Noren 2009). Estimating the cost of whale-watching 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 (Benoit-Bird & Whitlow 2003) or be derived indirectly from studies of stomach contents (Vikingsson 1997) or from inter-seasonal trends in energy storage (blubber thickness) (Vikingsson 1990). If those data are lacking, it can also, more vaguely, be informed by basic predation functional response types.

Once the link between behavioural changes and vital rates has been established, the next step is to identify which factors related to the whale-watching activities are the main drivers behind the behavioural changes, and focus management actions towards minimising these effects. Several factors related to the whale-watching activities, including distance to

the whales (Richardson et al. 1985), boat number (Williams & Ashe 2007), boat speed (Jensen et al. 2009) and boat behaviour (Williams et al. 2011), are likely to influence the perceived risk, and hence the response of the whale. In the absence of such data, whale watching should be considered as a black box (assuming that all interactions have the same effect), and exposure caps (upper limit of acceptable exposure to whale-watching boats) should be set to prevent potential long-term population effects.

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