

LETTER

Linking Behavior to Vital Rates to Measure the Effects of Non-Lethal Disturbance on Wildlife

Fredrik Christiansen^{1,2,3} & David Lusseau²¹ Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Warrnambool, VIC 3280, Australia² Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK³ Cetacean Research Unit, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, WA 6150, Australia**Keywords**

Anthropogenic disturbance; bioenergetics; cetacean; exposure; minke whale; non-consumptive effects; population consequences of disturbances; whalewatching.

Correspondence

Fredrik Christiansen, Deakin University/LES, Princes Highway, PO Box 423, Warrnambool, VIC 3280, Australia. Tel: +61-3-55633080; Fax: +61-3-52272019
E-mail: f.christiansen@live.se

Received

27 October 2014

Accepted

26 February 2015

Editor

Edward T. Game

doi: 10.1111/conl.12166

Abstract

The need for managing non-lethal effects on wildlife is becoming increasingly important as global human–wildlife interactions are now more frequent and more diverse. We developed a mechanistic model for minke whales (*Balaenoptera acutorostrata*) to measure the effects of behavioral disturbances caused by whalewatching activities on fetal growth. The model illustrates the pathway through which behaviorally mediated effects of anthropogenic disturbance might influence female reproductive success in an iteroparous capital breeding mammal. We found that although the behavioral disruptions caused by whalewatching interactions were substantial, the cumulative exposure of individuals to whalewatching boats was low, resulting in an effect on fetal growth no different from natural variability. This highlights the importance of considering all aspects of disturbance when evaluating effects of human disturbance on wildlife. Our mechanistic model can also be used to simulate different management scenarios to predict the long-term consequence of disturbance on vital rates, to help inform management decisions.

Introduction

Human interactions with wildlife can have both lethal (consumptive) and non-lethal (non-consumptive) effects on populations (Duffus & Dearden 1990; Boonstra *et al.* 1998; Peacor & Werner 2001). We have traditionally assumed that non-lethal impacts will have minor effects on population viability. However, a growing number of studies have shown that non-lethal effects can have similar, or even larger, influence on populations than direct mortality (Preisser *et al.* 2005; Creel *et al.* 2007). The cost of risks for an animal can be seen as a trade-off between investments in risk avoidance activities and other fitness activities, to reduce exposure to life threatening conditions (Lima & Dill 1990). If these costs are sufficient to reduce survival and/or reproductive success and affect enough individuals, risk can affect population dynamics. Animals make these decisions based on perceived rather

than actual risk, hence non-lethal human–wildlife interactions can elicit behaviorally mediated population effects (Frid & Dill 2002; Christiansen & Lusseau 2014). Our encroachment on wild places is increasing and diversifying (Messmer 2000), hence managing non-lethal interactions between humans and wildlife is becoming increasingly important. However, most existing management frameworks focusing on population level impacts have been developed to assess impacts from direct, lethal, effects of human–wildlife interactions (Wade 1998). We now need to integrate non-lethal impacts on wildlife population dynamics (Duffus & Dearden 1990).

Our current central management aims focus on conservation status, hence we need to manage impacts that have the propensity to affect population viability (Gill *et al.* 2001; NRC 2005). Non-lethal impacts are mediated by behavioral disruptions, which measured on their own do not provide much information about the biological

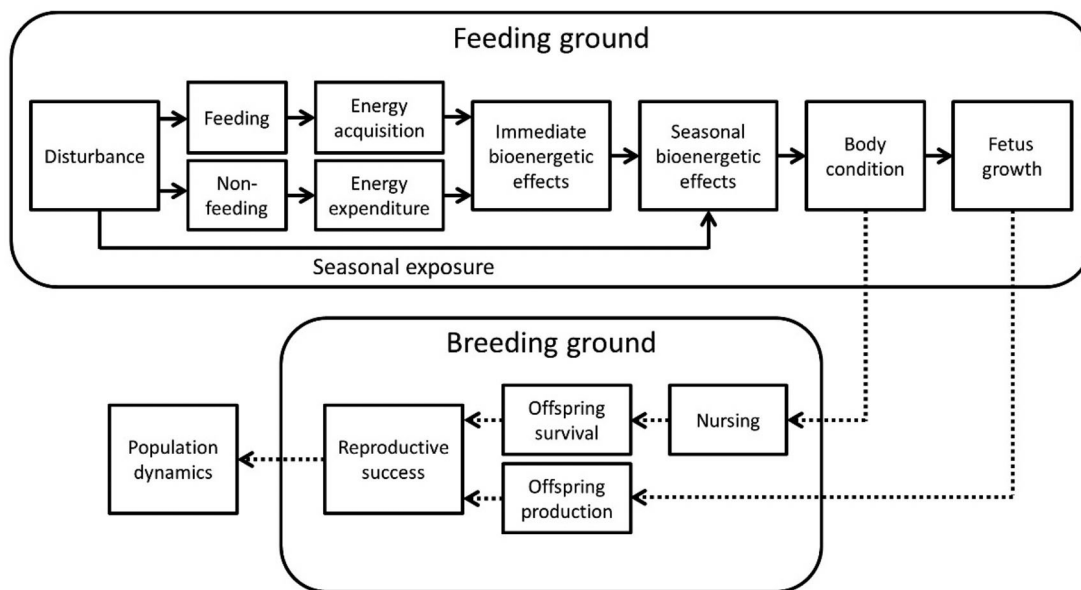


Figure 1 A mechanistic framework for linking short-term behavioral effects to long-term effects on individual vital rates for minke whales, with a focus on disturbance occurring on the feeding grounds. The modeling framework is designed for pregnant females to evaluate long-term effects on individual reproductive success. Solid links were informed in this study, whereas dotted links shows other potential pathways through which behaviorally mediated effects of anthropogenic disturbance might influence individual vital rates, and ultimately population dynamics.

importance of an impact (Beale & Monaghan 2004). We therefore need to understand how short-term behavioral effects of human disturbance translate into long-term biologically significant impacts on individual vital rates, so that management actions can be taken at an early stage to minimize risks for population viability (Gill *et al.* 2001). To do this, we need to understand the mechanisms leading to the population consequences of disturbances (PCoD) (Duffus & Dearden 1990; NRC 2005; New *et al.* 2014).

During the last two decades, the whalewatching industry has experienced a rapid growth worldwide, and as a result of this, most coastal cetacean populations are now being exposed to some form of whalewatching (O'Connor *et al.* 2009). Its sustainability is now called in question (Higham *et al.* 2014). The viability of some populations has been affected, with behavioral disruptions leading to a decrease in female reproductive success and a consequent decrease in population size (Lusseau *et al.* 2006; Currey *et al.* 2009).

In this study, we develop a mechanistic model for minke whales (*Balaenoptera acutorostrata*), a mysticete, in Faxaflói Bay, Iceland, a foraging ground, to measure the effects of whalewatching activities on fetal growth. Our model illustrates the pathway through which behaviorally mediated effects of anthropogenic disturbance might influence female reproductive success, and hence

vital rates, in a long-lived iteroparous capital breeding mammal. The model constitutes an essential component of a full PCoD model for marine mammals (New *et al.* 2014).

Methods

Developing a mechanistic model for whalewatching effects on minke whales

Cetaceans are K-selected species that are more likely to change their reproductive success before their survival when exposed to energetic constraints (Stephens *et al.* 2009). We focused on pregnant females, and the potential effect of whalewatching disturbance on their calf production (Figure 1). Baleen whales are capital breeders, which means that the foraging success of a female on the feeding ground will determine the amount of energy she can accumulate, in the form of body reserves, and later transfer to her offspring on the breeding grounds (Figure 1; Lockyer 2007). A decrease in foraging success caused by repeated foraging disruption is therefore likely to first have negative effects on maternal body condition (Figure 1). Behavioral disruptions can reduce the body condition of a female by increasing her energy expenditure and/or decreasing her energy acquisition (Figure 1; Williams *et al.* 2006). We therefore separated the activities of minke whales on the feeding grounds into

Table 1 Input parameters used to inform the model for whalewatching effects on minke whales in Iceland

Parameter	Unit	Mean	<i>n</i>	SD	Data type	Reference
Seasonal exposure (EXP)	Minute	427.5*	–	–	Photo-ID	a
Control foraging proportion (FOR _{Con})	%	15.26	1339	7.609	Behavioural	b
Impact foraging proportion (FOR _{Imp})	%	8.83	3301	5.813	Behavioural	b
Control energy expenditure (MR _{Con})	kJ kg ⁻¹ minute ⁻¹	56.5 × 10 ⁻³	57	21.2 × 10 ⁻³	Behavioural	c
Impact energy expenditure (MR _{Imp})	kJ kg ⁻¹ minute ⁻¹	72.2 × 10 ⁻³	56	21.2 × 10 ⁻³	Behavioural	c
Blubber deposition rate (BR)	m ³ day ⁻¹	2.44 × 10 ⁻³	48	0.334 × 10 ⁻³	Catch	d
Blubber density (BD)	kg m ⁻³	1.041 × >10 ³	–	–	Catch	e
Blubber energy content (BE)	kJ kg ⁻¹	29.05 × 10 ³	–	–	Catch	f
Body length (L)	m	7.53	191	0.815	Catch	d
Feeding season duration (T)	days	180	–	–	Abundance	g

*Represents the maximum estimated individual exposure

^aChristiansen *et al.* 2015.

^bChristiansen *et al.* 2013a.

^cChristiansen *et al.* 2014a.

^dChristiansen *et al.* 2013b.

^eParry 1949.

^fNordøy *et al.* 1995.

^gSigurjónsson & Víkingsson 1997.

feeding (activities leading to an overall net gain in energy) and non-feeding (activities leading to an overall net loss in energy) activities. We assessed how whalewatching interactions affect the proportion of time individuals spent in those two states (Figure 1). The cumulative bioenergetics costs from whalewatching interactions can be inferred by estimating how much time whales spent with boats through the feeding season (April 15 to October 13), given the cost of each interaction. We can then infer changes in body condition caused by these costs given the known energy requirement of pregnant whales in the feeding season (Figure 1). Although the body condition of an animal might also influence its behavioral response to disturbance (Beale & Monaghan 2004), for simplicity, we assumed that the behavioral effect was independent of body condition. We used blubber storage as a proxy for body condition, as blubber provides a good measure of energy balance of mysticetes (Miller *et al.* 2011; Christiansen *et al.* 2013b). We finally infer the effect of whalewatching disturbance on calf production by relating body condition losses to fetus developmental impacts (Figure 1). Importantly, this model accounts for the uncertainties associated with each estimation process to yield a confidence range for the effect of whalewatching disturbance on calf production.

Informing the links between behavior and vital rates

To inform the link parameters in our mechanistic model (Figure 1), we used empirically derived parameters from

a number of studies on minke whale behavioral ecology, physiology, and habitat use in Iceland (Table 1).

We estimated the relative decrease in feeding activity, ΔFOR (%), during interactions with whalewatching boats:

$$\Delta\text{FOR} = \frac{\text{FOR}_{\text{Imp}} - \text{FOR}_{\text{Con}}}{\text{FOR}_{\text{Con}}} \quad (1)$$

where FOR_{Imp} (%) and FOR_{Con} (%) are the proportions of time spent feeding in the presence (impact) and absence (control) of whalewatching boats, respectively. The corresponding increase in non-feeding activity, ΔNF (%), was:

$$\Delta\text{NF} = -\frac{\text{FOR}_{\text{Imp}} - \text{FOR}_{\text{Con}}}{100 - \text{FOR}_{\text{Con}}} \quad (2)$$

For simplicity, we assumed a linear relationship between feeding activity and energy acquisition and that the daytime activity budget of undisturbed whales (Christiansen *et al.* (2013a) (data were collected only between 6 a.m. and 6 p.m.) was also representative of night time activities. Based on this, the expected rate of energy acquisition, EA_{Imp} (kJ minute⁻¹), during interactions with whalewatching boats can be estimated:

$$\text{EA}_{\text{Imp}} = \text{EA}_{\text{Con}} \times (1 + \Delta\text{FOR}) \quad (3)$$

where EA_{Con} (kJ minute⁻¹) is the expected rate of energy acquisition (energy requirement) in the absence of boats, which can be estimated:

$$\text{EA}_{\text{Con}} = \text{MR}_{\text{Con}} \times W + \frac{\text{ED}}{60 \times 24} \quad (4)$$

where MR_{Con} is the rate of energy expenditure (kJ kg⁻¹ minute⁻¹) in the absence of boats, W is the body

mass (kg) of the whale and ED is the daily energy deposition (kJ day⁻¹) of pregnant minke whales through the feeding season. Body mass, W (kg), was estimated from the estimated length–mass relationship for minke whales (Folkow & Blix 1992):

$$W = 8.148 \times L^{3.163} \quad (5)$$

where L is the body length (m) of the whale. The daily energy deposition, ED (kJ day⁻¹), which represents the amount of energy per day that is deposited into the blubber layer of a pregnant minke whale through the feeding season, was estimated:

$$ED = BR \times BD \times BE \quad (6)$$

where BR is the average blubber deposition rate (m³ day⁻¹) for a pregnant minke whale through the feeding season, BD is the density of blubber (kg m⁻³), and BE is the energy content of blubber (kJ kg⁻¹).

From the estimates of EA_{Con} and EA_{Imp}, the rate of decrease in energy acquisition, ΔEA (kJ minute⁻¹), during whalewatching interactions could be estimated:

$$\Delta EA = EA_{Con} - EA_{Imp} \quad (7)$$

The change in rate of energy expenditure (metabolic rate), ΔMR (kJ minute⁻¹), during whalewatching interactions was estimated:

$$\Delta MR = (MR_{Imp} - MR_{Con}) \times W \times \left(1 - \frac{FOR_{Imp}}{100}\right) \quad (8)$$

where MR_{Imp} (kJ kg⁻¹ minute⁻¹) is the rate of energy expenditure during interactions. The expression $(1 - FOR_{Imp}/100)$ means that energy expenditure only increased, as a consequence of whalewatching, during non-feeding activity (the energy expenditure during feeding was assumed to be the same in the presence and absence of boats).

The immediate bioenergetic effects (net energy loss) of interactions, IEC (kJ minute⁻¹), was therefore:

$$IEC = \Delta EA + \Delta MR \quad (9)$$

Leading to the seasonal net energy loss, SEC (kJ):

$$SEC = IEC \times EXP \quad (10)$$

where EXP is the seasonal exposure (minute), or overall interaction time, for the most exposed minke whale.

We could then estimate the blubber volume of an impacted minke whale, BV_{Imp} (m³), at the end of the feeding season (October 13):

$$BV_{Imp} = BV_{Con} - \left(\frac{SEC}{EA_{Con} \times 60 \times 24 \times T}\right) \times BR \times T \quad (11)$$

where BV_{Con} is the expected blubber volume (m³) of an undisturbed female minke whale at the end of the feeding

season and T is the duration of the feeding season (days). BV_{Con} (m³) was estimated (Christiansen *et al.* 2013b):

$$BV_{Con} = -0.796 + 0.176 \times L + BR \times D \quad (12)$$

where D is the number of days into the feeding season (counted from April 27). The end of the feeding season (October 13) corresponds to $D = 168$.

From this we can estimate the relative body condition of an impacted female, FBC_{Imp} (%) (Christiansen *et al.* 2014b):

$$FBC_{Imp} = \frac{BV_{Imp} - BV_{Con}}{BV_{Con}} \quad (13)$$

Christiansen *et al.* (2014b) estimated the relationship between female body condition and fetus length from scientifically caught minke whales. We assumed that the cross-sectional observation that FBC reduction leads to reduced fetal growth applied to individual females. Based on this, the expected length of a fetus of an impacted female, FL_{Imp} (cm), at the end of the feeding season (October 13) was:

$$\log(FL_{Imp}) = 3.657 + 0.011 \times D + 0.994 \times FBC_{Imp} - 3.823 \times FBC_{Imp}^2 \quad (14)$$

Since FBC = 0 for an undisturbed female, the expected fetus length of an undisturbed female, FL_{Con} (cm), at the end of the feeding season is:

$$\log(FL_{Con}) = 3.657 + 0.011 \times D \quad (15)$$

We estimated the relative decrease in fetus length, ΔFL (%), at the end of the feeding season to assess the effect of whalewatching disturbance on fetal growth:

$$\Delta FL = \frac{FL_{Imp} - FL_{Con}}{FL_{Con}} \quad (16)$$

We defined the predicted reduction in growth rate as significant if the predicted fetal length at the end of the feeding season was below the 2.5% confidence limit for observed fetal length of an undisturbed female (FBC = 0) at this time (Christiansen *et al.* 2014b). There is theoretical evidence that decreased FL will decrease the probability of calf production (Christiansen *et al.* 2014b), but we currently have no empirical evidence to inform this relationship. Alternatively, a reduction in fetal growth could indirectly affect vital rates by reducing the size of the calf at birth (Kovacs & Lavigne 1986), and consequently offspring survival (McMahon *et al.* 2000), but again empirical data for minke whales are missing.

We estimated the mean of each link parameter in the mechanistic model and estimated standard deviations (SD) and 95% highest posterior density (HPD) intervals for each link parameter using bootstrapping resampling

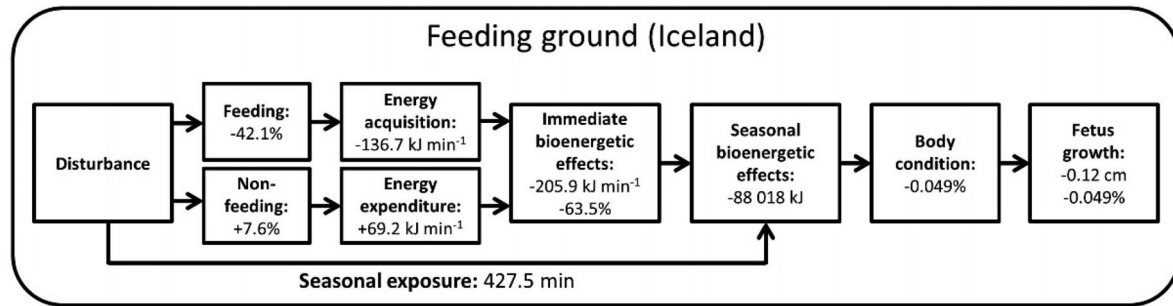


Figure 2 The informed mechanistic framework developed for minke whales in Iceland to link short-term behavioral effects to long-term effects on fetal growth, with whalewatching disturbance occurring on the feeding grounds. The measured effect sizes (means) for each link parameter in the mechanistic model are shown for each step in the model.

Table 2 Resulting link parameters from the mechanistic model for whalewatching effects on minke whales in Iceland. SD, standard deviation; HPDL, highest posterior density limit

Link parameter	Unit	Mean	SD	Lower 95% HPDL	Upper 95% HPDL
ΔFOR	%	-42.14	200.87	-100.00	117.98
ΔNF	%	7.59	12.85	-13.53	36.25
EA_{Con}	kJ minute^{-1}	324.40	147.37	88.02	633.12
EA_{Imp}	kJ minute^{-1}	187.71	806.09	0.00	822.49
ΔEA	kJ minute^{-1}	136.69	794.99	-497.38	558.20
ΔMR	kJ minute^{-1}	69.20	143.75	-209.88	366.26
IEC	kJ minute^{-1}	205.89	806.64	-428.27	791.01
SEC	kJ	88018.4	344838.2	-183083.5	338154.9
BV_{Con}	m^3	0.9392	0.1550	0.6326	1.2368
BV_{Imp}	m^3	0.9387	0.1549	0.6298	1.2356
FBC_{Imp}	%	-0.049	0.166	-0.220	0.136
FL_{Con}	cm	245.919	0	245.919	245.919
FL_{Imp}	cm	245.799	0.372	245.375	246.242
ΔFL	%	-0.049	0.151	-0.221	0.132

methods (Appendix S1). All calculations were performed using R 2.14.

Evaluating the long-term effects on minke whale vital rates

We used this mechanistic model to simulate the potential effect of whalewatching on fetal growth under different impact scenarios. We simulated different scenarios of activity state disruptions (the proportional increase in net energy loss in relation to net energy requirement, $\text{IEC}/\text{EA}_{\text{Con}}$) and seasonal exposure to whalewatching boats (EXP) to detect the conditions needed for whalewatching activities to have negative effects on fetal growth. We simulated net energy loss varying between 0% to 100% and daily boat exposure varying between 0 and 12 hours, whereas all other parameters of our mechanistic model were kept at their mean values.

Ethical consideration

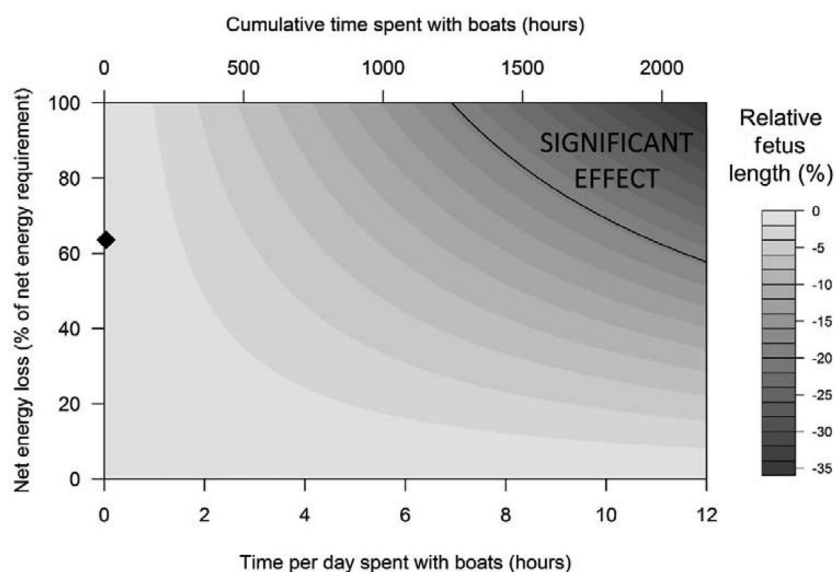
All the input parameters used to inform our mechanistic model came from published articles (Table 1). Because no

primary data were used for this study, no animal ethics clearance was required.

Results

Interactions with whalewatching boats resulted in a 42.1% (SD = 200.87) decrease in feeding activity and a 7.6% (SD = 12.85) increase in non-feeding activity (Figure 2 and Table 2, details of derivations in Appendix S2). This resulted in an estimated decrease in the rate of energy acquisition of $136.69 \text{ kJ minute}^{-1}$ (SD = 794.99) and an increase in energy expenditure of $69.20 \text{ kJ minute}^{-1}$ (SD = 143.75) (Figure 2). The estimated immediate bioenergetic effects of whalewatching interactions were therefore an overall net energy loss of $205.89 \text{ kJ minute}^{-1}$ (SD = 806.64), which is equivalent to 63.5% of the energy requirement of an undisturbed whale (EA_{Con}) (Figure 2). Despite this, the cumulative bioenergetic costs of whalewatching interactions for the most exposed individual (427.5 minute) only amounted to 88 018 kJ (SD = 344 838.2) in seasonal net energy loss (Figure 2). This led to a very small decrease in

Figure 3 Contour plot showing the effect of whalewatching disturbance on minke whale fetal growth under different impact scenarios. The effect on fetal growth is given as the relative decrease in fetus length at the end of the feeding season. In the simulations, the immediate bioenergetic effect of whalewatching interactions (the proportional increase in net energy loss in relation to net energy requirement) and the seasonal exposure to whalewatching activities (the number of hours per day spent with boats) were artificially varied from 0% to 100% and from 0 to 12 hours, respectively. The solid black line indicates the threshold value (−18.4%) below which whalewatching will have a significant effect on fetal growth. The black diamond at the left margin indicate the present whalewatching scenario in Faxaflói Bay, Iceland (a 63.5% decrease in net energy intake and a seasonal exposure of 427.5 minutes (0.04 hours per day)).



female body condition of 0.049% (SD = 0.166) at the end of the feeding season (Figure 2). The resulting decrease in fetus length at the end of the season was only −0.049% (SD = 0.151). This is well below the set threshold value for a significant effect on fetal growth (−18.4%).

Female minke whales would have to spend a large proportion of their day with whalewatching boats, every day of the feeding season, for those to start having a biologically important effect on fetal growth (Figure 3).

Discussion

The mechanistic model developed in this study illustrates the pathway through which behaviorally mediated effects of anthropogenic disturbance might influence individual vital rates in minke whales. This model can easily be adapted to other species, both marine and terrestrial, to evaluate PCoD. As the ways in which we interact with wildlife are diverse (e.g. urbanization, wildlife tourism, industrialization of wild places) and more intense nowadays, such mechanistic modeling frameworks are urgently needed to understand and manage human disturbance on wildlife. Our case study highlights the importance of taking all aspects into consideration when evaluating PCoD. The immediate behavioral changes caused by the presence of whalewatching boats resulted in a 63.5% decrease in net energy intake. However, the number of boat interactions experienced by individuals throughout the feeding season was very low, so that the estimated effect on fetal growth was negligible. Thus, we can conclude that at its current capacity, the whalewatching industry in Faxaflói Bay is

unlikely to have a significant effect on minke whale calf production.

A reduction in calf production can be estimated as “takes” in a population model (Figure 1). The resulting PCoD approach would then provide a framework to manage non-lethal disturbances as any other consumptive activity (Duffus & Dearden 1990; Tremblay 2001), and further put tourism into context with other consumptive activities (e.g., fisheries bycatch). However, although uncertainties surrounding the number of direct takes can be quantified relatively easily (e.g., by using observer programmes), quantifying the number of animals (i.e., fetuses) that may die as a result of disturbance will be much harder. Some links in our mechanistic framework (Figure 1) might not be directly quantifiable and may only be possible to inform using expert elicitation methods (Martin *et al.* 2012). How to deal with such wide confidence limits also needs to be determined. Despite these obstacles, developing such a management framework would be a worthwhile effort, since it would offer an avenue to manage behaviorally mediated effects on populations using existing approaches to focus on regulatory targets such as population viability (Wade 1998).

Although effects on vital rates in cetaceans are more likely to be caused by a reduction in reproductive success (Lusseau *et al.* 2006; Currey *et al.* 2009), adult survival is likely to have a larger influence on population dynamics in long lived, slow breeding species (Benton & Grant 1999). Behavioral compensation could also be incorporated into our mechanistic model by adding a feedback mechanism between body condition and behavior, the magnitude of which could be determined by the

species ecological (e.g., prey availability) and biological constraints (e.g., reproductive strategy) (Christiansen & Lusseau 2014). Similarly, the body condition of an animal might also influence its response to whalewatching disturbance (Beale & Monaghan 2004).

The within-year effects of whalewatching on minke whale fetal growth are determined by the energetic costs incurred during a whalewatching encounter and the total number of such encounters an individual whale experiences during the course of the feeding season (Figure 3). If whales were exposed to whalewatching boats throughout the day (12 hours), a 60% net energy loss during interactions, which is close to the present effect size, would be sufficient to have significant effects of fetal growth. Management can impose changes to boat behavior during interactions to potentially reduce the immediate bioenergetic effect size or reduce the number of hours of boat interactions per day experienced by individual whales (e.g., by operating over a larger area or reduce the number of trips per day). However, the current whalewatching scenario in Faxaflói Bay is far from having a significant effect on minke whale fetal growth (Figure 3).

Because of their large population size (Skaug *et al.* 2004), migratory behavior and inter-bay movement (Vikingsson & Heide-Jørgensen 2005), the individual exposure of minke whales to whalewatching in Iceland is relatively low compared with other cetacean populations globally. In contrast, many small and resident populations (predominantly odontocetes) are exposed to repeated and prolonged interactions with whalewatching across daylight hours and for most of the year (Williams *et al.* 2006; Christiansen *et al.* 2010). With some of these populations already showing population-level consequences from whalewatching disturbance (Bejder *et al.* 2006; Lusseau *et al.* 2006; Currey *et al.* 2009), we urge wildlife managers to make use of our mechanistic modeling framework to better understand the mechanisms and drivers of these effects, to help inform management decisions.

Acknowledgments

Funding was received from the University of Aberdeen, Graduate School Competitive Studentship grant scheme and the Marine Alliance for Science and Technology for Scotland pooling initiative. We are grateful for the constructive comments provided by Dr Amanda Lombard and two anonymous reviewers.

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