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Effects of whale watching vessels on adult male sperm whales off Andenes, Norway

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ABSTRACT

This study investigated the effects of whale-watching vessels (WWV) on solitary sperm whales off Andenes in northern Norway. The presence of WWV did not have a significant effect on the duration of the surface and foraging dive periods, nor on the respiration pattern and dynamics. The presence of WWV, however, made sperm whales almost seven times more likely to perform a near surface event (NSE). NSEs are submersions without fluking for short periods of time that take place during the surface phase. The occurrence of NSEs led to a significant increase of 75% in surface time, that is 6 more minutes at the surface which were not compensated with longer foraging dives. Additionally, the occurrence of NSEs was associated with changes in the animals' respiration pattern and dynamics. Data collection concerning NSEs and respiration dynamics (both parameters assessed here for the first time) is strongly recommended in future impact studies on this species. NSEs may be indicators of disturbance and are reasonably easy to identify, and thus identifying and better understanding the causes of this behavior have management implications.

INTRODUCTION

Whale-watching is a growing form of wildlife tourism. Over 13 million people go whale and dolphin watching in 119 countries every year (O'Connor, Campbell, Cortez, & Knowles, 2009), generating over USD$ 2.1 billion in revenues, directly and indirectly (e.g., travel expenses and accommodation). However, the increased interaction between cetaceans and whale-watching vessels has raised concerns over the potential impact of the activity. Short-term effects have been reported worldwide for many cetacean species. The presence of whale-watching vessels has been associated with changes in surface behavior and changes in activity and energy budgets, including reduction of resting and foraging bouts (Lusseau, 2003b; Constantine, Brunton, & Dennis, 2004; Lusseau, 2004; Williams, Trites, & Bain, 2006; Whaley, Wright, Bonnelly de Calventi, & Parsons, 2007; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008; Stamation, Croft, Shaughnessy, Waples, & Briggs, 2009; Lusseau, Bain, Williams, & Smith, 2009; Visser *et al*., 2011).

In Norway, the whale-watching industry has been growing at an annual rate of about 5% (O'Connor *et al*., 2009; Dutton, 2011; IWC 2011), with over 35000 visitors in 2008 (O'Connor *et al*., 2009). The two largest companies are based in Andenes and Stø, in the Vesterålen archipelago in Northern Norway (Fig. 1), and, together with a third operator (also based in Andenes), conduct daily trips in the same waters during the summer months. The main targeted species is the sperm whale (*Physeter macrocephalus)*. This is one of the only three locations in the world where whale-watching is focused on adult male sperm whales, together with Japan and New Zealand (Hoyt, 2001; O'Connor *et al*., 2009).

Only solitary adult male sperm whales inhabit high latitudes, as it is the case off Andenes, in northern Norway (e.g., Letteval *et al*., 2002). These males migrate back to breeding areas in warmer waters, although the frequency and routes of those migrations remain unknown. Roving males and sexual dimorphism indicates size-dependent male competition (Whitehead, 1994), thus high energetic returns are needed in order to reach and maintain a greater size. This could explain why males migrate to distant feeding grounds in high productivity areas, such as the deep waters of the Bleik canyon in Northern Norway (Sundby, 1984).

Studies on the impact of whale-watching vessels on the behavior of solitary, adult, male sperm whales in feeding grounds have been carried out off the coasts of Kaikoura, in New Zealand. The presence of whale-watching vessels has been associated with more erratic breathing, changes in the inter-breath interval and reduced surface time (Gordon, Leaper, Hartley, & Chappell, 1992; Richter, Dawson, & Slooten, 2003, 2006; Markowitz, Richter, & Gordon, 2011). These authors also mentioned that whales would occasionally "shallow dive" when disturbed (e.g., during close vessel approaches). The term "shallow dive" was coined by Gordon *et al*. (1992) who described it simply as "diving without fluking". Given the potential for confusing this term with dives in shallow waters, this behavior (studied here for the first time in an impact study) has been renamed as "near surface event" (NSE).

In previous studies, encounters where sperm whales performed a NSE were terminated (i.e., not further monitored) and data was excluded from further analysis (Gordon *et al*., 1992; Richter *et al*., 2003, 2006; Markowitz *et al*., 2011). These NSEs are short underwater periods that do not involve foraging (i.e., the whales are not clicking) and appear to interrupt resting and normal oxygen intake. They also appear to entail an unnecessary increase in energy expenditure, especially when accompanied by an avoidance behavior. Alterations in the behavioral budget resulting in reduced energy intake or increased energy expenditure affect the overall energetic budget, and thus potentially the fitness of the individual or population (e.g., Lusseau, 2004; Lusseau &Bejder, 2007).

This study investigates the effects of whale-watching vessels on the behavior of solitary, adult, male sperm whales off Andenes. To that end, and to allow for comparison with previous studies on adult male sperm whales off Kaikoura (Gordon *et al*., 1992; Richter *et al*., 2003, 2006; Markowitz *et al*., 2011), data were collected on the respiration pattern and dynamics as well as on the duration of surfacings and foraging dives. Additionally, data were collected on the occurrence and duration of NSEs. Both, NSEs and the respiration dynamics were assessed here for the first time in an impact study for sperm whales. Lastly, consideration is given to whether the observed short-term effects could have long-term consequences for the individuals.

The results of this study are important to the understanding of sperm whales' behavioural response to disturbance and have implications for the management of the activity, both in the study area and beyond.

MATERIAL AND METHODS

Study area

This study was conducted in waters off Andenes, in Northern Norway. On the northwest side of Andøy Island there is a deep submarine canyon known as Bleik Canyon that reaches depths of near 2000 m towards the end of the continental shelf, and where sperm whales have been found historically (Ciano & Huele, 2001; Hvalsafari unpublished). On the east side of the island there is a 350-500 m deep fjord, known as Andfjord, where whales have also been encountered in recent years (Hvalsafari, unpublished data) (Fig. 1).

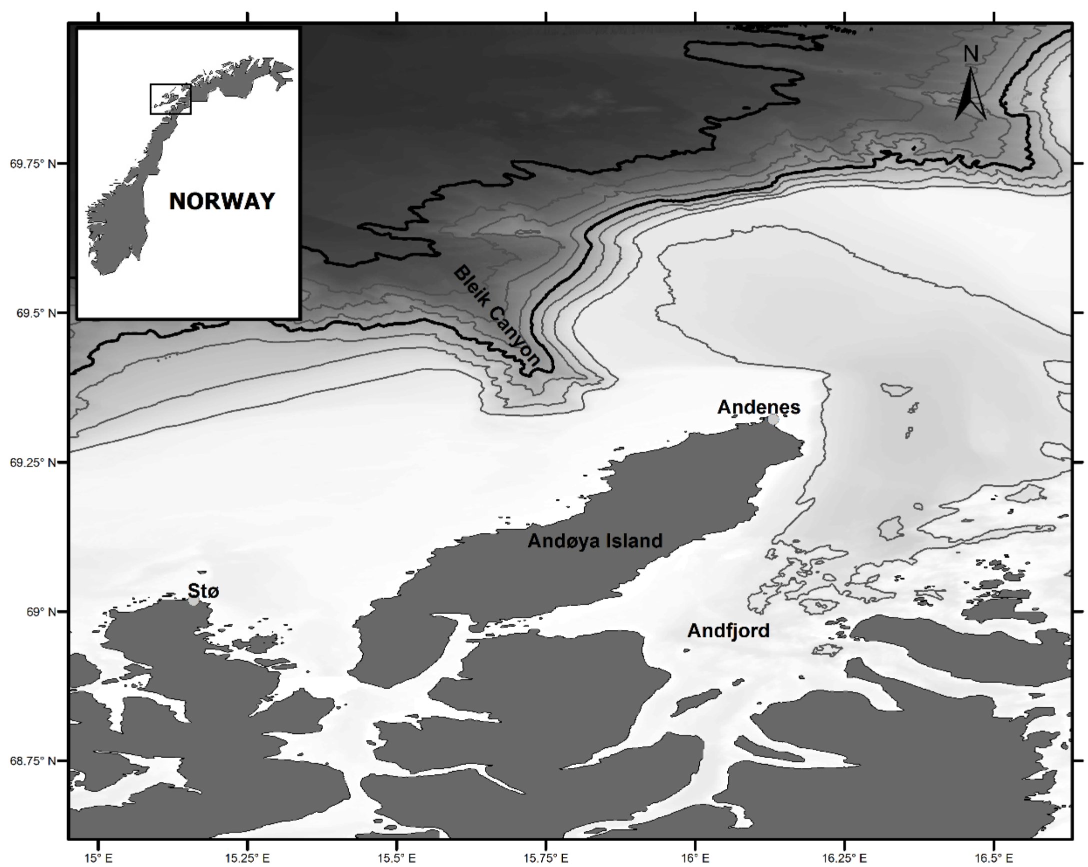

Figure 1: Location and detailed map of the study area in Northern Norway. Whale-watching trips depart from Andenes and Stø. Contour interval is 250 m; thicker lines show 1000 m and 2000 m respectively.

Data collection

Data was collected during the summer months of 2012 on board a 28.46 m whale-watching vessel that was used as an opportunistic research vessel (hereafter "research vessel"). The research vessel typically conducted two trips per day. Depending on weather conditions, before the first trip of the day (and when required), a land-based observer scanned the study area using Bigeyes® binoculars (25X, 80mm). Land-based observers were trained by an experienced observer (i.e., the author). Location of animals at sea was approximated through the use of an internal reticule system (i.e., distance) and a graduated wheel (i.e., bearing), and the approximate distance and direction to the animals were then provided to the team on the vessel.

Onboard the research vessel, whales were tracked acoustically using two mounted directional hydrophones. The incoming signals were monitored by an operator equipped with a pair of headphones. Due to stereo-effect, the operator would determine whether a given signal was on the port side or the starboard side. The vessel would turn slowly to the side where the signal is stronger. The procedure would be repeated until the signal on both hydrophones is equally strong, when the bearing to the whale would simply be the heading of the vessel. The stronger the signal, the closer the whale (Nielsen and Møhl, 2006). As sperm whales in the study area typically cease clicking a few minutes before surfacing, it was possible to anticipate when the whale that was being monitored was about to surface. Given that there were at least two observers onboard the research vessel, it is fair to assume that the whale was spotted as soon as, or right after, it appeared on the surface. When whales were spotted, small movements were made to reposition the vessel parallel to the whale and (not directly) behind it, to allow for a proper photo-ID of the individual.

During every whale encounter and using an Olympus Recorder WS-750M, the following data were collected: weather conditions (sea state, wind speed and direction); time of surfacing and time of dive (i.e., fluking) to calculate the duration of surfacing; duration of foraging dives (i.e., time between fluking and resurfacing) to the nearest minute, when two consecutive sightings of the same whale occurred; inter-breath intervals (to the nearest second) to study the respiration pattern and dynamics (described below); and the occurrence of near surface events (NSE). NSEs are considered a component of the surface phase of the sperm whale foraging bouts and were used as a covariate. Additionally, coordinates were recorded using a portable Garmin eTrex GPS. These coordinates were used both to map the sightings (Fig. 2) as well as to obtain water depth as described below.

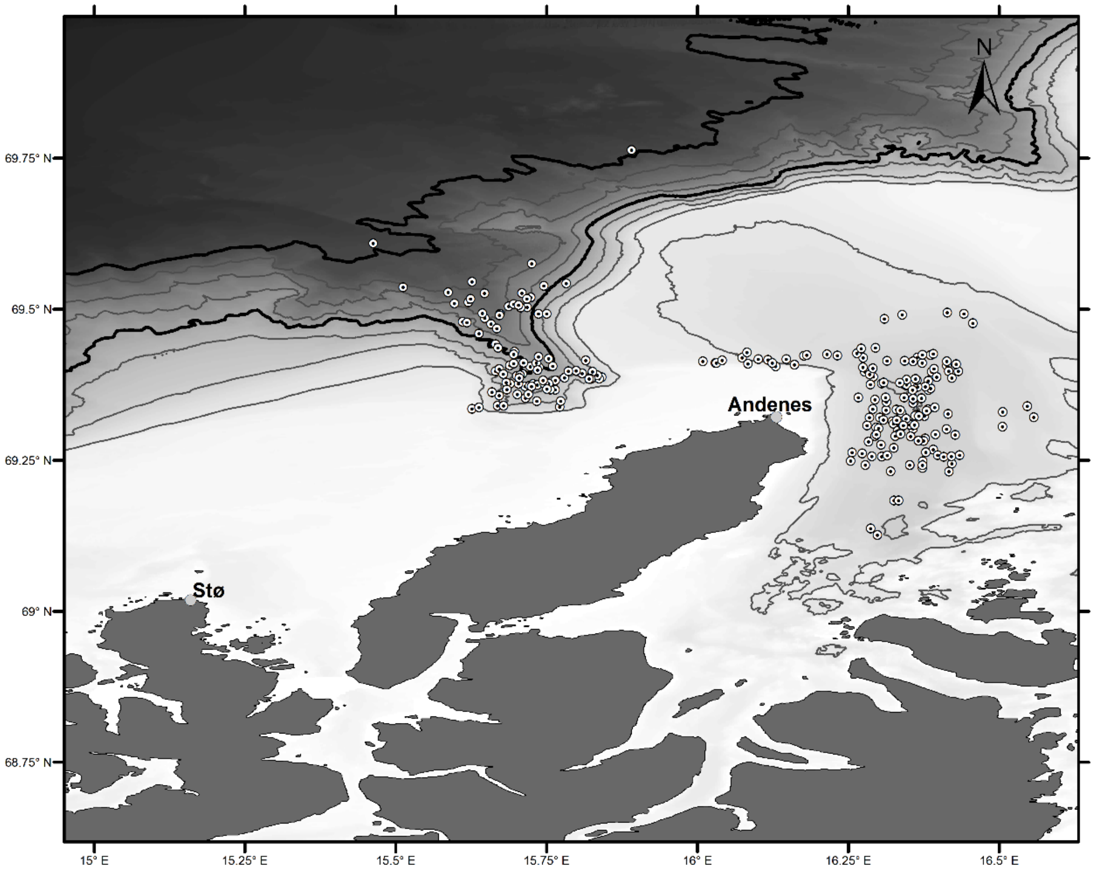

Figure 2: Sightings of sperm whales (*Physeter macrocephalus*) in the study area (*n* = 247). Contour interval is 250 m; thicker lines show 1000 m and 2000 m respectively.

Lastly, when the whale fluked, pictures of the dorsal and ventral side of the fluke were taken for photo-identification purposes using a Canon 1000D SLR camera fitted with a 70-300mm Canon lens or a Canon EOS 40D fitted with a 28-135mm Canon lens. Fluke images from each trip were organized and edited using Adobe Photoshop CS5. When an individual was first observed in the season, it was given a consecutive identification number (*ID*), 1 being the first whale identified in the season.

A sighting was considered to be "in the presence of a whale-watching vessel" (WWV) when a WWV approached and remained within the impact zone, defined as 300 m around the focal whale (the distance was estimated by eye by the captain of the vessel, who has over 25 years of whale watching experience). The impact zone was determined arbitrarily, given that there are no whale-watching regulations in the area.

In all cases solitary individuals were followed. On one occasion two whales were within the impact zone at about 100 m from each other. No interaction between them was observed, hence these sightings were analyzed independently from each other.

Analysis

Each follow was given a consecutive *follow number*, 1 being the first follow of the season. Using latitude and longitude at dive, water depth (in m) was extracted from a shape file (downloaded from GEBCO (IOC, IHO &BODC, 2003)) using R (version 3.0.1; R Development Core Team 2013). Packages used: *adehabitat* (Calenge, 2006) and SDMTools (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2008).

Pictures were matched against the catalog of individuals previously identified in the season.

All statistical analyses were made using R (Packages *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & the R Development Core Team, 2013) and *lme4* (Bates, Maechler, & Bolker, 2011)). Graphical exploration indicated that no data transformation was required (i.e., the assumptions of homocedasticity and normality of residuals were met).

- *Surface behavior*

Occurrence of near surface events (NSEs)

The *occurrence of NSEs* during a given encounter follows a binomial distribution (i.e., presence/absence). In order to investigate if the presence of WWV had an influence in the probability of a whale performing a NSE, a mixed-effect logistic regression model was used, with *WWV presence* as the predictor variable and *ID* as the random factor to account for individual variability (i.e., heterongeneity of variance) and pseudoreplication (Hurlbert, 1984).

Duration of the surface period

When studying the factors influencing the *duration of the surface period*, linear mixed models were used with the following predictor variables (i.e., fixed effects): *sea state* (i.e., environmental conditions), *water depth* (i.e., ecological factor) and *presence* and *number of WWV* (i.e., potential stressors). Additionally, and in order to investigate any associated behavioral response, *the occurrence of NSEs* was used as a covariate. The individual *ID* was used as a random factor. The same models with *follow number* within *ID* as a random factor were used to account for temporal correlation.

Respiration pattern and dynamics

The respiration pattern is described by the *number of blows per follow*, the inter-breath intervals (*IBI*) and its standard deviation. Two linear mixed effect model with *WWV presence* and *occurrence of NSEs* as fixed effects, and *ID* as the random factor were used to investigate if the predictor variables had an effect on the *number of blows* per follow.

The *IBI* is the time elapsed between two consecutive blows during the surface phase. A subset was created removing blow intervals corresponding to shallow dives (30 out of 6193), under the assumption that the inclusion of those intervals would affect the interpretation of results regarding mean *IBI* and its standard deviation. Subsequently, four linear mixed effect models with *WWV presence* and *occurrence of NSEs* as fixed effects and *ID* as the random factor were used to investigate if the predictor variables had an effect on *IBI* and its standard deviation per follow.

The respiration dynamics is the variation of the *IBI* throughout the surface period, and it is described by 'blow number' in the *x* axis and the standardized *IBI* (i.e., *IBI*/mean interval for that follow) in the *y* axis. Therefore, each blow was given a consecutive blow number, *1* being the first blow immediately before diving, and the standardized *IBI* for each blow number per follow was estimated (Gordon *et al*., 1992).

It was not possible to model the respiration dynamics due to its complexity, thus a non-parametric test (Kolmogorov-Smirnov 2-sample) was performed. The predictor variables considered were the presence of WWV and the *occurrence of NSEs*. To that end, the joint respiration dynamics of all observations made in the presence of WWV was compared to those in the absence of WWV (i.e., only the research vessel present); similarly, the respiration dynamics of all observations where whales performed a NSE was compared to those where the whale did not performed a NSE.

-*Foraging dives*

To study the factors affecting the *duration of foraging dives*, linear mixed models were used with the following predictor variables (i.e., fixed effects): *sea state* (i.e., environmental conditions), *water depth* (i.e., ecological factor) and *WWV presence* and *number of WWV* (i.e., potential stressors). Additionally, and in order to investigate any associated behavioral response, *the occurrence of NSEs* was used as a covariate. The same models with *follow number* within *ID* as a random factor were used to account for temporal correlation. Lastly, the *number of blows* (as a proxy for oxygen intake) and *duration of the surface period* (i.e., recovering/preparation period) were used as covariates.

The individual *ID* was used as a random factor. The same models with *follow number* within *ID* as a random factor were used to account for temporal correlation.

- *Model selection*

Model selection was based on the Akaike Information Criterion (AIC), retaining those models with the smallest AIC numbers. Akaike weight of ith model (ω_i, how likely it is that the ith model is the best model given the data) was used to retain or discard models with higher AIC numbers. During the model selection process, model validation tests were run to identify potential violations of the underlying assumptions of the models.

- *Level of exposure*

Based on data from this study and personal communication with other companies in the area, an approximate level of exposure for each whale per season was estimated. To that end, the total number of individually identified whales during the season (*n* = 64) and the whale-watching days per season, as well as the number of daily trips per vessel and whale encounters per trip were used.

RESULTS

Data was collected over 78 days, from the 1st of June until the 14th of September 2012. In total 247 individual follows were selected, 95 of which were in the Bleik Canyon (Fig. 2). In 39.3% (*n* = 97) of follows, sightings were in the presence of at least one WWV. Whales in this study were individually monitored from 1 to 39 occasions (mean = 5.75, median = 3), in 1 (*n* = 13) to 17 different days.

All 247 follows were used to study the respiration pattern and dynamics, while only follows where whales were identified, representing 40 individuals, were used in surface models (*n* = 230). In 89 encounters the whale was monitored for a full dive cycle (i.e., surfacing and the following foraging dive) representing 26 different whales, thus this data was used in foraging dive models.

A total of 64 whales were individually identified in this study and this number was used to estimate individual whale exposure to whale-watching in the season (see "*Level of exposure*").

Surface behavior

- Occurrence of *NSEs*

In 11.7% (n=29) of follows the whale performed at least one NSE. The overall probability of a whale performing a NSE during a given observation was 0.065 (95% CI = 0.031 to 0.129). The mean duration of NSEs was 3.11 ± 3.2 min (SD), ranging from 24 to 921 sec. Whales that performed a NSE were seen once or more during the season and were similarly distributed over the study area. The presence of WWV had a significant effect in the probability of a whale performing a NSE (χ^2 = 10.78, p = 0.001), increasing the probability from 0.026 (95% CI = 0.008 to 0.096) to 0.171 (95% CI = 0.078 to 0.284).

Model validation suggested that some factors not accounted for in this study were also influencing the occurrence of NSEs (see discussion).

- Duration of the surface period

Although the *duration of the surface period* increased by a few seconds in the presence of WWV, the effect was not significant ($F_{1.189}$ = 0.432, p = 0.511). The model that best fitted the data includes exclusively *the occurrence of NSEs* (Table 1), which had a significant effect ($F_{1.189}$ = 82.03, $p < 0.001$), increasing the expected surface time (8.01 min, SE = 0.28) by 6.05 min (SE = 0.66).

Table 1: *Physeter macrocephalus*. Selection of models explaining the duration of the surface period (n = 247). LME = linear mixed effect model, AIC = Akaike's information criterion. ω_i = weight of evidence for each model. NSE = occurrence of near surface events. ID = individual identification number

Model	Model type	Fixed effects	Random effects	df	AIC	ΔAIC	ωi
1	LME	Depth + Sea state + NSE	ID	6	1162.023	5.515	0.039
2	LME	Sea state + NSE	ID	8	1163.031	3.524	0.108
3	LME	Depth + NSE	ID	5	1161.506	1.999	0.229
4	LME	NSE	ID	4	1159.507	0	**0.624**

- Respiration pattern and dynamics

The number of blows per follow was not affected by *WWV presence* ($F_{1,189}$ = 1.09, p = 0.297) or the *occurrence of NSEs* ($F_{1,189}$ = 0.91, p = 0.34). The presence of WWV did not have a significant effect on the *IBI* or its standard deviation either. However, the *IBI* and its standard deviation were significantly affected in those follows where the whale performed a NSE (Table 2).

Table 2: *Physeter macrocephalus*. Respiration pattern. Linear mixed effect models with ID as a random effect. NSE = occurrence of near surface events. ID = individual identification number. (Blow intervals representing NSE were excluded).

#	Response variable	Fixed effects	AIC	Estimate	Slope	F_{df}	p
1	Interval (sec)	WWV presence	37641.27	17.85±0.45	-0.28±0.15	F_{6122} = 3.63	0.056
2	Interval (sec)	NSE	37445.6	17.12±0.48	3.92±0.27	F_{6122} = 208.54	**<0.001**
4	Standard deviation	WWV presence	967.18	4.20±0.24	0.16±0.26	F_{189} = 0.374	0.541
5	Standard deviation	NSE	950.7	4.06±0.21	1.77±0.42	F_{189} = 17.34	**<0.001**

The *IBI* varied throughout the surface period as expected (Gordon *et al.*, 1992), becoming longer as time progresses but shortening immediately before fluking (Fig. 3). The result of the non-parametric Kolmogorov-Smirnov (2-sample) test showed that the presence of WWV did not have a significant effect ($p = 0.08$) on the respiration dynamics while the *occurrence of NSEs* did ($p < 0.0001$) (Fig. 4).

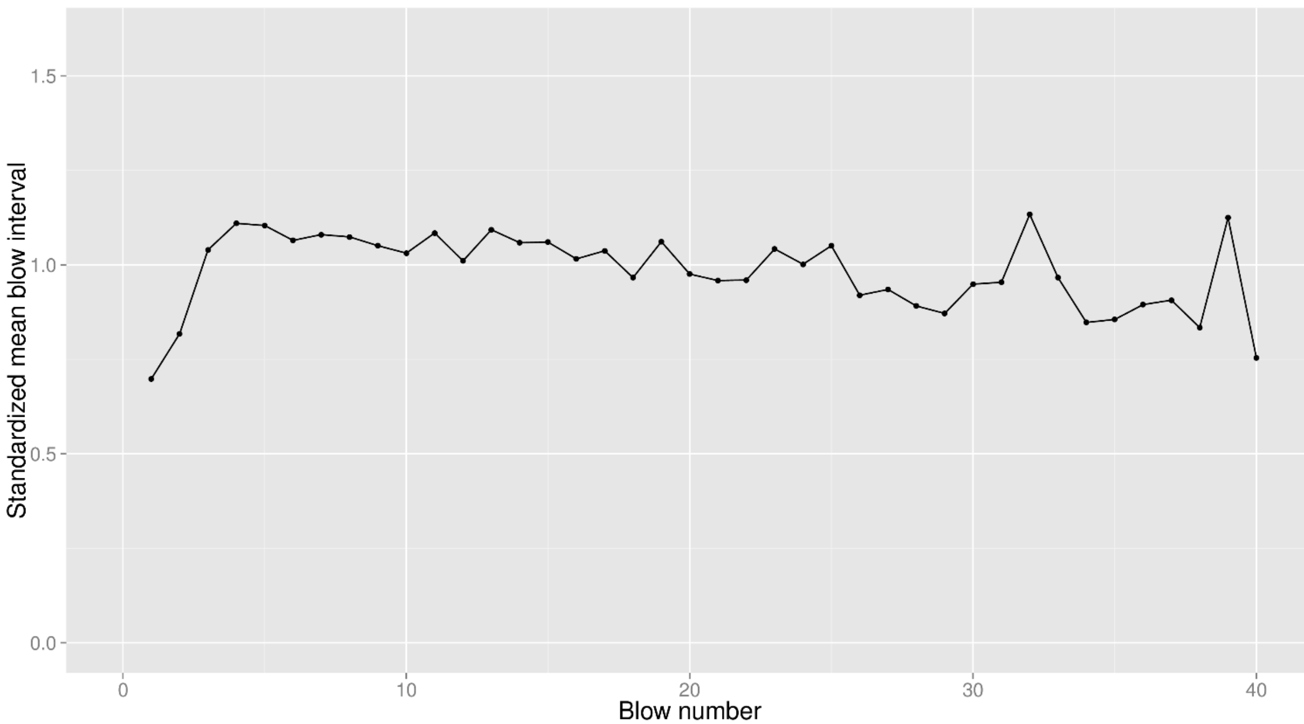

Figure 3: *Physeter macrocephalus*. Respiration dynamics. Blow number against mean values of standardized inter-breath intervals (IBI). Standardized intervals are IBI divided by the mean IBI for that individual follow. Time runs backwards (i.e. the whale dives at blow number 0) and each point represents the mean of all the standardized intervals for that given blow number. Peaks represent long shallow dives (n = 247).

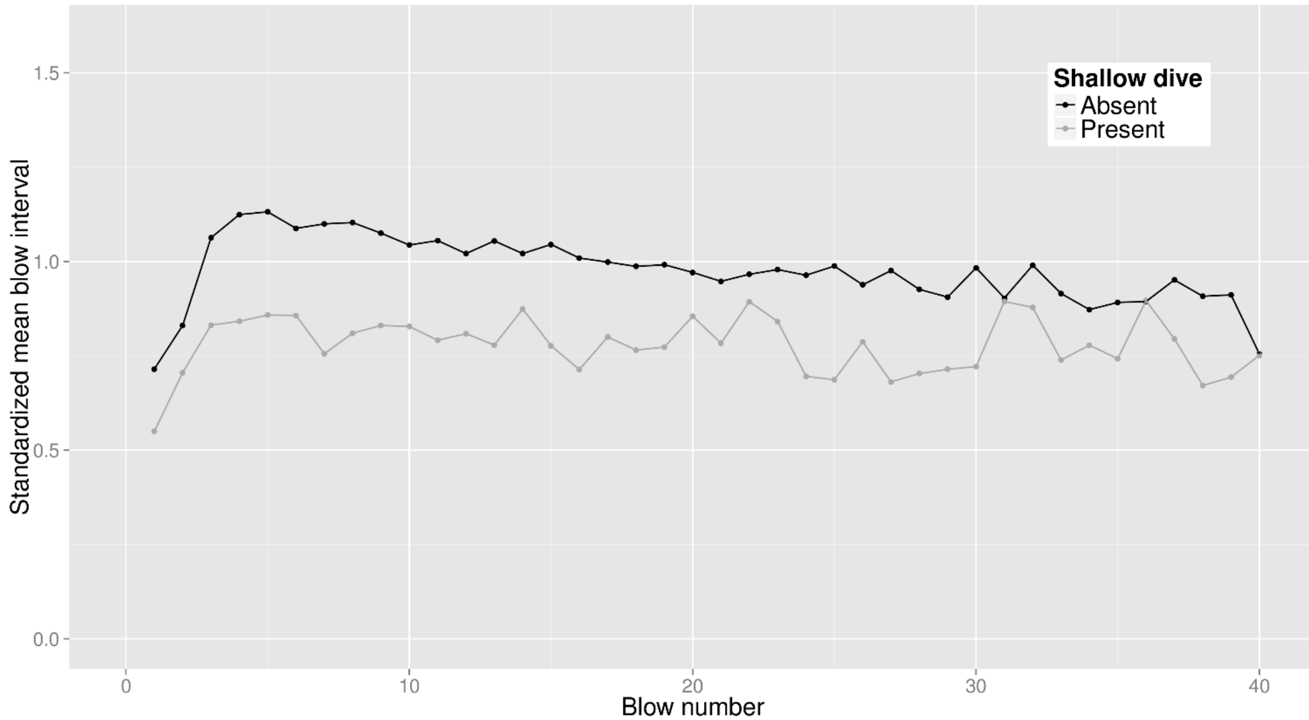

Figure 4: *Physeter macrocephalus*. Respiration dynamics. Graphical comparison of the respiration dynamics between encounters with and without the occurrence of shallow (intervals corresponding to shallow dives were removed). Blow number against mean values of standardized inter-breath intervals (IBI). Standardized intervals are IBI divided by the mean IBI for that individual follow. Time runs backwards (i.e. the whale dives at blow number 0) and each point represents the mean of all the standardized intervals for that given blow number. Peaks represent long shallow dives (*n* = 247).

Foraging dives

One whale that spent a total of 13.7 min at the surface (including a NSE of almost 2 min) performed a 55 min foraging dive. Based on the assumption that the long dive was not a response to compensate for the NSE when at the surface, this data// point was removed from further analyses in order to avoid misinterpretation of results.

The model that provided more information about the *duration of the foraging dive* given the data (i.e., lowest AIC), was the null model (i.e., with no independent variables). The other models had less support (Table 3). The estimated dive duration was 29.11±0.88 min (SE). The second best model was the one with *water depth* as the only predictor variable, although it did not have a significant effect on the duration of the dive ($F_{1,61}$ = 1.35, p = 0.2488). The mean *water depth* where the whales started their foraging dives was 418.54 ± 252.96 m. *Water depth* ranged from 97 to 1965 m, and it was greater than 1000m only in 11 occasions.

Table 3: *Physeter macrocephalus*. Selection of models explaining the duration of the foraging dive (*n* = 88). LME = Linear mixed effect model, AIC = Akaike's information criterion, ω_i = weight of evidence for each model. NSE = occurrence of near surface events. ID = individual identification number

Model	Model type	Fixed effects	Random effects	Df	AIC	ΔAIC	ω_i
1	LME	Surface time	ID	4	558.140	3.523	0.086
2	LME	WWV presence	ID	4	558.122	3.505	0.086
3	LME	NSE	ID	4	558.121	3.504	0.086
4	LME	Nr of blows	ID	4	558.032	3.415	0.09
5	LME	Depth	ID	4	556.974	2.357	0.153
6	LME	~1	ID	3	554.616	0	**0.498**

Level of exposure

During the summer season all tour vessels taken together approximate 1860 sightings. Given that approximately 30% of encounters will include at least two vessels, only 1302 encounters represent one individual whale and at least one vessel (i.e., the research vessel or a whale-watching vessel). Thus, each whale will be in the presence of at least one vessel an average of 20.34 times during a given summer season and it would perform a NSE less than twice (1.38 times).

The average number of times a given whale is encountered per season presented here might be overestimated given that it is likely that there are more whales in the study area than those encountered (n = 64) by the vessel used as a research platform during this study. On the other hand, some whales may be encountered more often as discussed below.

DISCUSSION

Behavioral changes due to human disturbance has been reported for several cetacean species, such as bottlenose (e.g., Lusseau, 2003a,b, 2004; Constantine *et al*., 2004), common (e.g., Stockin *et al*., 2008) and Risso's dolphins (Visser *et al*., 2011), killer (e.g., Williams *et al*., 2006; Lusseau *et al*., 2009), humpback (e.g., Whaley *et al*., 2007; Stamation *et al*., 2009) and sperm whales (e.g., Gordon *et al*., 1992; Richter *et al*., 2003; Magalhães *et al*., 2002; Markowitz *et al*., 2011). The risk-disturbance hypothesis argues that animals perceive human disturbance in a similar manner to nonlethal predation risk, and thus an animal’s response should follow the same economic principles as if encountering a predator (Frid &Dill, 2002), as observed, for example, in elk (Becker, Moi, Maguire, Atkinson, & Gates, 2012) and birds (Peters &Otis, 2005; Blumstein, Fernández-Juricic, Zollner, & Garity, 2005). Sperm whales do not seem to follow this principle, exhibiting various acoustic and behavioral reactions (and sometimes no reaction at all) to natural (Wright, 2003) and anthropogenic underwater sounds (e.g., Madsen &Møhl,

2000; Madsen, Møhl, Nielsen, & Wahlberg, 2002), to the presence of whale-watching platforms (e.g., Magalhães *et al*., 2002; Richter *et al*., 2003) and to killer whale presence/sounds (i.e., predators) and attacks (e.g., Pitman, Ballance, Mesnick, & Chivers, 2001; Curé *et al*., 2013; Hvalsafari unpublished data). It appears that sperm whales may react less to the presence of tour vessels than other cetacean species, with recent studies only reporting changes in the inter-breath intervals (IBI) (e.g., Richter *et al*., 2006; Markowitz *et al*., 2011). On the other hand, impact studies conducted on the species so far have not accounted for NSEs or variations in the respiration dynamics.

The variations of the IBI per follow, and its standard deviation, do not adequately describe the respiration dynamics in sperm whales given that the IBI naturally varies throughout the surface period (Gordon &Steiner, 1992; Gordon *et al*., 1992; this study) (Fig. 3). This variation was first described in undisturbed whales off the Azores (Portugal) by Gordon and Steiner (1992), who proposed that blow intervals becoming longer may reflect carbon dioxide being removed from the body and oxygen reserves replenishing achieving maximal oxygen levels, whilst the increased respiration rate just before fluking could be a hyper-ventilation to reduce carbon dioxide levels (cited in Gordon *et al*., 1992). In this study, neither the described dynamics, nor the mean IBI, its standard deviation or the number of blows per follow were found to be significantly affected by the presence of WWV.

A more evident behavioral response are NSEs (e.g., Gordon *et al*., 1992; Richter *et al*., 2006) and this is the first time, to our knowledge, that this parameter is included in an impact study. Whales were almost 7 times more likely to perform a NSE in the presence of WWV, leading to a significant increase of 6 min (75%) in surface time. The difference between the mean duration of a NSE (~ 3 min) and the additional time spent at the surface has two possible explanations: a) some individuals performed more than one NSE per surfacing affecting the mean increase in surface time b) sperm whales may need time to recover from the NSE before engaging in a foraging dive.

In previous studies, when sperm whales performed a NSE, the observation was terminated and not included in further analyses; however, the resurfacing was analyzed as a complete surface period, possibly affecting the results and its interpretation. This seems to be the case in Richter *et al*. (2003), who found a minimum surface time of 6 sec for an adult male sperm whale off Kaikoura. Also, Gordon *et al*. (1992) reported 10% of encounters ending with a NSE and found a 17% reduction of the surface time in the presence of WWV, together with a positive correlation between surface and dive durations, suggesting that longer dives require longer times at the surface. If, as in Richter *et al*. (2003), resurfacings were treated as full surface phases, the reduction in surface time found by Gordon *et al*. (1992) may be the result of discarding data regarding NSEs.

A previous study on sperm whales off Andenes (Teloni *et al*., 2008) found that the mean duration of foraging dives in individuals not exposed to whale-watching was similar (~32 min) to that found in this study. The authors also found that 72% of these foraging dives were in depths less than 400m. Based on the buzz production they proposed that during those dives whales target epipelagic prey, feeding on more sparsely distributed prey items (i.e., most likely fish instead of cephalopods) than during deeper and longer dives (Teloni *et al*., 2008).

The results of the present study suggest that the duration of the foraging dives is independent of all the studied predictor variables, including the presence of WWV, water depth and duration of the previous surface period. Additionally, the occurrence of NSEs did not lead to longer dives; hence, the additional time spent at the surface due to NSEs represents time that will no longer be available for other activities, such as foraging and resting. It is possible, however, that whales performed dives only a few seconds longer each time (i.e., compensating throughout the day or season), or that significantly longer dives were performed randomly (i.e., not detected with the factors used in our models), or that significantly longer dives occurred during times when animals were not followed. Nevertheless, this time loss, under the current level of exposure, represents only about 12 min loss in an entire season. It is thus unlikely to be biologically significant as discussed below.

Sperm whales have a low cost of living, low diet quality (Spitz *et al*., 2012) and one of the highest diving efficiencies reported for a diving animal (Watwood, Miller, Johnson, Madsen, & Tyack, 2006). Their foraging strategies are related to their specific energetic requirements (Spitz *et al*., 2012) and the behavior of their prey (e.g., Davis *et al*., 2007; Fais *et al*., 2015), therefore, performing longer dives might not be worth the effort. Changes in behavior leading to reduced energy intake or increased energy use, can negatively affect the energy budget of the individuals (Lusseau, 2003b), which in turn can affect the reproductive success of individuals (Steven, Pickering, & Castley, 2011), and, potentially, the survival of the population.

It is noteworthy that when whales performed NSEs in this study they also showed more erratic breathing and changes in the respiration dynamics (Fig. 4). It is unknown whether these observed associated behavioral responses are due to NSEs, or that NSEs are a consequence of disturbing a whale that is already distressed. At least some bird species change their response to human disturbance according to their individual state and the state of the environment (Beale & Monaghan, 2004), and cetaceans have also been observed to change their behavior depending on which behavior they are engaged in (e.g., Lusseau, 2003a; Lundquist, Gemmell, & Würsig, 2012). It was not, however, the purpose of this study to make analyses that were redundant for whales that already showed signs of disturbance, but to present a more holistic approach.

The results of this study also suggest that some factors not accounted for may also influence the occurrence of NSEs. For instance, Gordon *et al*. (1992) and Richter *et al*. (2003) reported that transient sperm whales off Kaikoura showed a stronger reaction to the presence of WWV than resident individuals. The low level of re-sightings found in this study could indicate that also this area is visited by both resident and transient individuals. Future research should aim at understanding the circumstances under which whales are more likely to perform NSEs, and the relationship with other anthropogenic factors (e.g., vessel handling, speed of approach), internal factors specific to that whale (e.g., duration of the previous dive, resident/transient individual) or a combination of both. In the interim, and given that NSEs are easy to identify (i.e., the whales simply 'disappear' underwater), whales that engage in NSEs should be abandoned by whale-watching vessels to reduce disturbance levels.

Land-based follows were not attempted because of the local rapid changing weather conditions and an inability to determine if two consecutive surfacings corresponded to the same whale. Thus, it is possible that the whale-watching vessel that used as an opportunistic research platform may have had an effect on the animals. On the other hand, mean surface and foraging dive durations found in this study are consistent with the findings of Teloni *et al*. (2008), who tagged four whales in the Bleik Canyon which were not exposed to tourist (or any other) vessels. Additionally, the results do show significant changes in the presence of other WWVs, suggesting that the research vessel was a suitable observation platform to contrast behavioral changes.

Long term consequences

During the summer season, whale-watching trips are conducted on a daily basis (weather allowing) from 9am to around 9pm. The results of this study suggest that a whale would be encountered about 20 times during a given summer season and, thus, it would perform NSEs less than twice per season. Nonetheless, currently only two out of six vessels use hydrophones to locate whales, thus it is normal practice to remain in the area where the first animal was seen, as well as to return on the following trip. As a result the same individual may be targeted several times a day by more than one whale-watching vessel.

Sperm whales may be present in waters off Andenes year round (Hvalsafari, unpublished data). And although the residency patterns of individual whales are unknown, some males have been repeatedly encountered within and between years. Consequently, some sperm whales could be repeatedly targeted over the course of a season, performing NSEs more often than expected and suffering reduced energy intake. Under the current level of exposure, however, it is unlikely that such a reduction would have detrimental consequences for the energetic budget of individuals.

When this study was conducted, the whale-watching season was carried out only during the summer months. However, since 2011 whale-watching has also been carried out during the winter months. Although mainly targeting killer, humpback and fin whales, it also targets sperm whales when the other species are not readily accessible.

CONCLUSIONS AND RECOMMENDATIONS

The presence of whale-watching vessels had a statistically significant effect on sperm whales' behavior while at the surface, making them more likely to perform near surface events (NSEs). These NSEs led to an increase in surface time that was not followed by longer foraging dives, and were associated with changes in the pattern and dynamics of respiration. Such short-term effects likely do not have biological consequences for the individuals under the current level of exposure. However, a larger number of whale--watching vessels in the area and the development of the winter season could increase the occurrence of the observed short-term effects and potentially lead to long-term consequences. The use of hydrophones as well as increased collaboration between companies, especially with the use of the land-based station, can help avoid targeting the same individual. Sperm whales that show signs of disturbance (e.g. NSEs) should be avoided, minimising or preventing the adverse consequences of cumulative effects.

Near surface events are an easy to identify indicator of likely disturbance, and thus they could be included in regulations or protocols of whale-watching targeting sperm whales. Hence, the collection of further data concerning NSEs and respiration dynamics are strongly recommended in future impact studies on sperm whales, as these data may well help explain the circumstances under which obvious and subtle responses occur in the presence of whale-watching vessels or other potential stressors

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REFERENCES

Bates, D., Maechler, M., and Bolker, B. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.

Beale, C.M., and Monaghan, P. 2004. Behavioural responses to human disturbance: a matter of choice? *Anim Behav*, *68*(5):1065–1069. doi:10.1016/j.anbehav.2004.07.002

Becker, B.H., Moi, C.M., Maguire, T.J., Atkinson, R., and Gates, N.B. 2012. Effects of hikers and boats on tule elk behavior in a national park wilderness area. *Human-Wildlife Interactions*, *6*(1):147–154.

Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A., and Garity, S.C. 2005. Inter-specific variation in avian responses to human disturbance. *J Appl Ecol 42:*943–953.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Mod 197*:516-519.

Ciano, J.N. and Huele, R. 2001. Photo-identification of sperm whales at Bleik canyon, Norway. *Mar Mam Sci 17*(1):175-180.

Constantine, R., Brunton, D.H., and Dennis, T.E. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conserv*, *117*:299–307.

Curé, C., Antunes, R., Alves, A.C., Visser, F., Kvadsheim, P.H., and Miller, P.J.O. 2013. Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Sci Rep*, *3*:1579. doi:10.1038/srep01579

Davis, R., Jaquet, N., Gendron, D., Markaida, U., Bazzino, G., and Gilly, W. 2007. Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. *Mar Ecol Prog Series*, *333*:291–302. doi:10.3354/meps333291

Dutton, A. 2011. Norwegian use of whales: past, present and future trends. Report to WSPA. Available at: http://www.dyrsrettigheter.no/wp/wp-content/uploads/NORWEGIAN-USE-OF-WHALES-PAST-PRESENT-AND-FUTURE-TRENDS.pdf

Fais, A., Aguilar Soto, N., Johnson, M., Pérez-González, C., Miller, P.J.O., and Madsen, P.T. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behav Ecol Sociob*. doi:10.1007/s00265-015-1877-1

Frid, A., and Dill, L. 2002. Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conserv Ecol*, *6*(1):11. Available at http://www.consecol.org/vol6/iss1/art11

Gordon, J. and Steiner, L. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. *Rep Int Whal Comm 42:*561–565.

Gordon, J., Leaper, R., Hartley, F.G. and Chappell, O. 1992. *Effects of whale watching vessels on the surface and underwater acoustic behavior of sperm whales off Kaikoura, New Zealand*. Science and Research Series No. 52. Department of Conservation, Wellington, New Zealand. 64 pp.

Hoyt, E. 2001. *Whale watching 2001: worldwide tourism numbers, expenditures and expanding socioeconomic benefits*. International Fund for Animal Welfare, Yarmouth Port, UK.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr 54*(2):187–211.

International Whaling Commission. 2011. Annual Report of the Scientific Committee of the International Whaling Commission. 63rd Meeting held in Tromsø, Norway, in May 2011.

IOC, IHO and BODC. 2003. Centenary Edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, U.K.

Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., McCall Howard, P. 2002. Social structure and residency in aggregations of male sperm whales. *Can J Zool*, *80*(7):1189–1196. doi:10.1139/Z02-102

Lundquist, D., Gemmell, N.J., and Würsig, B. 2012. Behavioural responses of dusky dolphin groups (*Lagenorhynchus obscurus*) to tour vessels off Kaikoura, New Zealand. *PloS One*, *7*(7):e41969. doi:10.1371/journal.pone.0041969

Lusseau, D. 2003a. Male and female bottlenose dolphins *Tursiops spp*. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Mar Ecol Prog Ser*, *257*:267–274. doi:10.3354/meps257267

Lusseau, D. 2003b. Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conserv Biol*, *17*(6):1785–1793. doi:10.1111/j.1523-1739.2003.00054.x

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecol Soc*, *9*(1):2.

Lusseau, D., and Bejder, L. 2007. The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment. *Int J Comp Psych 20*(2-3):228–236.

Lusseau, D., Bain, D., Williams, R., and Smith, J. 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales Orcinus orca. *Endang Sp Res, 6*(3):211–221. doi:10.3354/esr00154

Madsen, P.T., and Møhl, B. 2000. Sperm whales (*Physeter catodon* L. 1758) do not react to sounds. *J. Acoust. Soc. Am 107*(1):668–671.

Madsen, P.T., Møhl, B., Nielsen, B. K., and Wahlberg, M. 2002. Male sperm whale behaviour during exposures to distant seismic survey pulses. *Aq Mamm*, *28*(3):231–240.

Magalhães, S., Prieto, R., Silva, M.A., Gonçalves, J., Afonso-Dias, M., and Santos, R.S. 2002. Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. *Aq Mamm*, *28*(3):267–274.

Markowitz, T., Richter, C. and Gordon, J. (Eds). 2011. *Effects of tourism on the behavior of sperm whales inhabiting the Kaikoura Canyon.* Report submitted to the New Zealand Department of Conservation by PACE-NZRP, Kaikoura Sperm Whale and Tourism Research Project.

Nielsen, B.K. and Møhl, B. 2006. Hull-mounted hydrophones for passive acoustic detection and tracking of sperm whales (*Physeter macrocephalus*). *Appl Acoust 67*:1175-1186

O'Connor, S., Campbell, R., Cortez H. and Knowles, T. 2009. *Whale watching worldwide: Tourism numbers, expenditures and expanding economic benefits*. International Fund for Animal Welfare. Yarmouth, MA, 265pp.

Peters, K.A., and Otis, D.L. 2005. Using the risk-disturbance hypothesis to assess the relative effects of human disturbance and predation risk on foraging American oystercatchers. *The Condor*, *107*:716–725.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and the R Development Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1- 109.

Pitman, R.L., Ballance, L.T., Mesnick, S.I., and Chivers, S.J. 2001. Killer Whale Predation on Sperm Whales: Observations and Implications. *Mar Mamm Sci*, *17*(3):494–507. doi:10.1111/j.1748-7692.2001.tb01000.x

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Richter, C.F., Dawson, S.M., and Slooten, E. 2003. Sperm whale watching off Kaikoura, New Zealand: Effects of current activities on surfacing and vocalisation patterns. *Sci Conserv*, *219*:5-78.

Richter, C.F., Dawson, S., and Slooten, E. 2006. Impacts of commercial whale watching on male sperm whales at Kaikoura, New Zealand. *Mar Mamm Sci*, *22*(1):46–63.

Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., and Ridoux, V. 2012. Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. *PloS One*, *7*(11):e50096. doi:10.1371/journal.pone.0050096

Stamation, K.A., Croft, D.B., Shaughnessy, P.D., Waples, K.A., and Briggs, S.V. 2009. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. *Mar Mamm Sci*, *26*(1):98–122. doi:10.1111/j.1748-7692.2009.00320.x

Steven, R., Pickering, C., and Castley, G.J. 2011. A review of the impacts of nature based recreation on birds. *J Environ Manag*, *92*(10):2287–94. doi:10.1016/j.jenvman.2011.05.005

Stockin, K., Lusseau, D., Binedell, V., Wiseman, N., and Orams, M. 2008. Tourism affects the behavioural budget of the common dolphin *Delphinus sp*. in the Hauraki Gulf, New Zealand. *Mar Ecol Prog Series*, *355*:287–295. doi:10.3354/meps07386

Sundby, S. 1984. Influence of bottom topography on the circulation at the continental shelf off Northern Norway. *Fiskeridirektoratets Skrifter. Serie Havundersøkelser 17*:501-519.

Teloni, V., Johnson, P.M., Miller, J.O.P. and Madsen, T.P. 2008. Shallow food for deep divers: Dynamic foraging behavior of male sperm whales in a high latitude habitat. *J Exp Mar Biol Ecol*, *354*(1):119–131. doi:10.1016/j.jembe.2007.10.010

Van Der Wal, J., Falconi, L., Januchowski, S., Shoo, L., and Storlie, C. 2008. Species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. R package. Version 1.1-13.

Visser, F., Hartman, K.L., Rood, E.J.J., Hendriks, A.J.E., Zult, D.B., Wolff, W.J., Huisman, J., Pierce, G.J. 2011. Risso's dolphins alter daily resting pattern in response to whale watching at the Azores. *Mar Mamm Sci*, *27*(2):366–381. doi:10.1111/j.1748-7692.2010.00398.x

Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T., and Tyack, P.L. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol*, *75*(3):814–825. doi:10.1111/j.1365-2656.2006.01101.x

Whaley, A. R., Wright, A.J., Bonnelly de Calventi, I., and Parsons, E.C.M. 2007. Humpback whale sightings in southern waters of the Dominican Republic lead to proactive conservation measures. *Mar Biodiv Rec* 1: e70, 1–3.

Whitehead, H. 1994. Delayed competitive breeding in roving males. *J Theor Biol*, *166*:127–133.

Whitehead, H. 2009. Sperm whale: *Physeter macrocephalus*. In W. F. Perrin B. Würsig and J. G. M. Thewissen, (Eds), *Encyclopedia of marine mammals*, 2nd edition (pp 1091-1097). San Diego, CA: Elsevier

Williams, R., Trites, A.W., and Bain, D.E. 2006. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *J Zool*, *256*(2):255–270. doi:10.1017/S0952836902000298

Wright, A.J. 2003. *The effects of a tropical storm on the use of clicks by sperm whales in the northern Gulf of Mexico*. Master's Thesis, University of Wales, Bangor. 147pp.