



Increased proximity of vessels reduces feeding opportunities of blue whales in the St. Lawrence Estuary, Canada

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ABSTRACT: Blue whales *Balaenoptera musculus* occur seasonally in the St. Lawrence Estuary, Canada, where they spend most of their time foraging. Their recurrent presence has stimulated the development of a large whale-watching industry. Here, we examine the effect of vessel distance on blue whale foraging behaviour by measuring changes in surface and diving patterns. Vessels were within 2000 m of blue whales during 70 % of 33 follows, and 59 % of total observation time. At vessel distances ≤ 400 m, surface and dive times were on average 49 and 36 % shorter, respectively, and the number of breaths taken by the whales was reduced by 51 % compared to control observations without vessel presence within 2000 m of whales. The consequent reduction in foraging time was likely greater than 36 %, given that transit time is incompressible and foraging depth is dictated by where krill densities are located. We showed that the relative proportion of lost foraging time from vessel exposure increased exponentially with prey depth. Whales were unable to compensate for lost feeding opportunities by increasing diving rate or swim speed, except when feeding within 10 to 15 m of the surface. Our results indicate that preventing vessels from entering within a 400 m radius around blue whales can help reduce the negative effects of marine recreational activities on blue whale foraging.

KEY WORDS: Disturbance · Behaviour · Whale-watching · Foraging · GLMM · GEE

INTRODUCTION

Vessel traffic may alter marine mammal behaviour through their physical presence, elevated underwater noise levels and exposure to collision risks (Richardson et al. 1995, Laist et al. 2001, Nowacek et al. 2007, Clark et al. 2009, Parsons 2012, Pirotta et al. 2015). Whale-watching, a form of vessel traffic in which boat operators and tourists specifically seek to interact with marine mammals, is a lucrative business that has developed rapidly and widely over the past decades (O'Connor et al. 2009). This type of activity has been repeatedly shown to elicit short-term be-

havioural responses from a variety of marine mammal species (e.g. Richardson et al. 1995, Parsons 2012, Senigaglia et al. 2016 for reviews). Such changes in behaviour can result in increased energetic expenditures or decreased energetic gains (e.g. Gordon et al. 1992, Christiansen et al. 2014). When repeated or persistent, these activities have the potential to affect vital rates through changes in activity budget, loss of foraging opportunities, or reduction in mate or predator detection capacity by loss of acoustic space (e.g. Bejder et al. 2006, Williams et al. 2006, Lusseau & Bejder 2007, Clark et al. 2009, Christiansen et al. 2013a,b, Symons et al. 2014).

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Measuring short-term behavioural reactions of targeted individuals to vessel exposure is a common method to evaluate the effects of whale-watching and other activities. Often, the degree of response is inferred from changes in respiratory and diving patterns, activity budget, acoustic behaviour or movement metrics (Southall et al. 2007, Parsons 2012, Senigaglia et al. 2016). Marine mammals are air-breathing vertebrates, and thus behave as central-place foragers, where the surface acts as the central place to which they must return after foraging trips at depth (Orians & Pearson 1979, Kramer 1988). For most marine mammals, the time spent at the surface replenishing oxygen stores has a positive influence on the time they can allocate at depth during a subsequent foraging dive (Kooyman & Ponganis 1998, Thompson & Fedak 2001). Therefore, in cases where foraging represents the predominant activity, metrics related to respiratory patterns and dive time can be reasonable proxies for estimating loss of feeding opportunities associated with vessel interaction and the potential effects on vital rates (e.g. Christiansen & Lusseau 2015).

Blue whales *Balaenoptera musculus* are considered capital breeders, provisioning their offspring using energy stores accumulated over earlier periods (Houston et al. 2007). During the fattening period, blue whales and other cetaceans occupy the St. Lawrence Estuary, Canada, where they spend most of their time feeding (Lesage et al. 2007, Doniol-Valcroze et al. 2012). High and recurrent densities of these cetaceans during the summer and fall have stimulated the development of a whale-watching industry consisting of approximately 40 vessels, offering several departures per day. Whale-watching and other recreational activities are regulated within the limits of the Saguenay-St. Lawrence Marine Park (see Fig. 1), where there are prohibitions for vessels to be within 400 m of whales listed as endangered or threatened under the Canadian Species at Risk Act, such as the blue whale and St. Lawrence Estuary beluga *Delphinapterus leucas* (Canada Gazette 2015a). In sectors outside the marine park, where most of the blue whale aggregations are located, whale-watching and other recreational activities are regulated via the Marine Mammal Regulations of the Fisheries Act, which prohibits disturbance without specifying a distance limit (Canada Gazette 2015b).

To assess the adequacy of the 400 m limit for mitigating potential effects from whale-watching and other vessel interactions on foraging blue whales, we report on their short-term behavioural responses to vessel proximity, using variables related to breathing

and diving patterns. Empirical relationships between surface time, foraging time and the number of feeding opportunities while at depth have been documented for St. Lawrence Estuary blue whales (Doniol-Valcroze et al. 2011). Considering that foraging is their predominant activity in this area, with on average 68% of their time spent in this activity (T. Doniol-Valcroze & V. Lesage unpubl. data), the chosen metrics are relevant for inferring losses of feeding opportunities as a result of vessel interactions.

MATERIALS AND METHODS

This study was conducted between July and September of 2006 and 2010, during peak blue whale abundance (Edds & MacFarlane 1987) and whale-watching activities (Chion et al. 2009) in the St. Lawrence Estuary, Canada. Our study area corresponded to the sector located over the Laurentian Channel, between Cap Colombier and Grandes-Bergeronnes (Fig. 1). Weather permitting (i.e. Beaufort sea state ≤ 3 and > 2 km visibility), a portion of this sector was searched for the presence of blue whales. The searched area was changed daily to ensure complete coverage of the study area at regular intervals. Observations were made from a 10 m rigid-hull inflatable vessel that was either moving at very low speed (< 3 km h⁻¹) or completely stationary.

Only 1 whale was followed at a time, and none of the followed individuals were part of a group as this would have led to uncertainty when measuring individual breathing and diving parameters. An observer was specifically tasked with recording the time of each breath taken by the focal animal. A second observer estimated the whale's position relative to our research vessel (i.e. its distance using naked eye or a range finder, and angle relative to magnetic north using binoculars with an integrated compass) at the beginning and end of each breathing sequence. At the end of each breathing sequence, this observer also noted the number and type of vessels other than our own (i.e. small or larger tour boat, recreational vessels, or merchant ships) that were observed within the following estimated distance categories from the focal whale: 0–400, 400–1000, 1000–2000, and > 2000 m. In addition, the observer estimated the distance of the closest vessel to the whale at the time of its last breath; this distance was validated *a posteriori* using radar positioning of the vessel, and the whale's estimated position to allow further analysis of proximity effects, including categories within 0 to 400 m (e.g. see Fig. 2). Distance

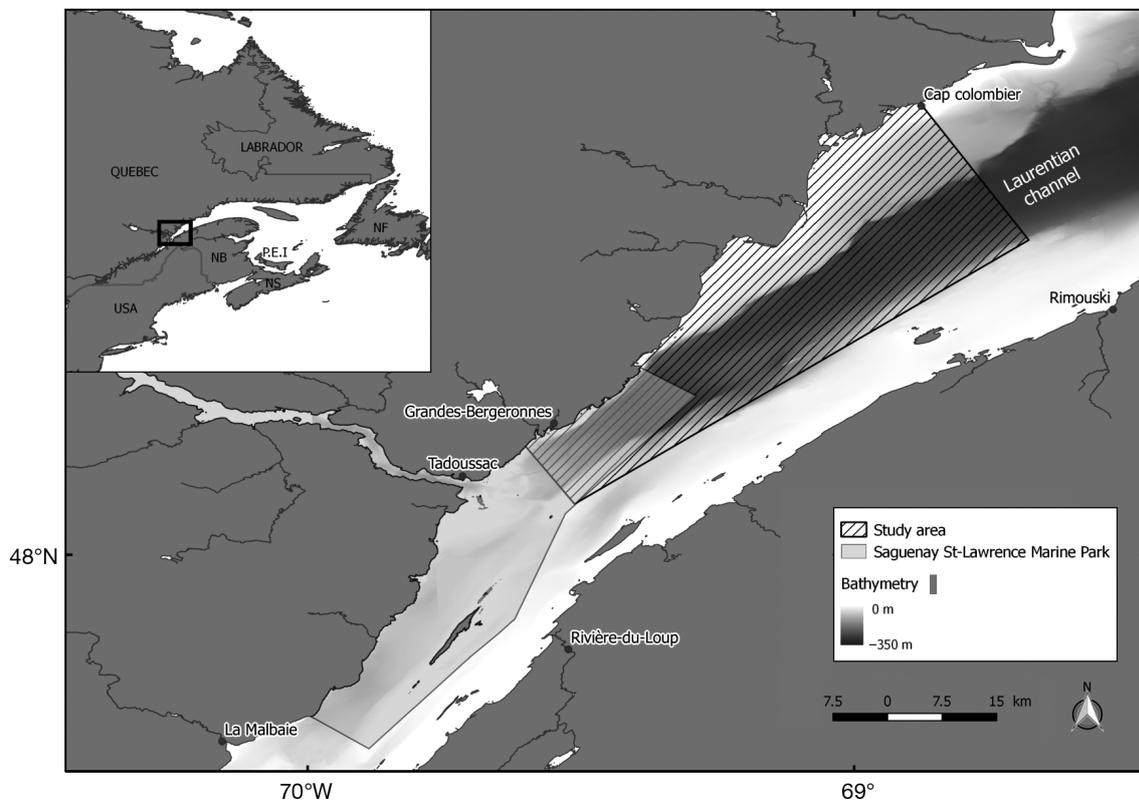


Fig. 1. Study area in the St. Lawrence Estuary, eastern Canada

estimates made by the naked eye were periodically calibrated with distances to objects or vessels measured using the radar system. A radar operator monitored vessel movements using target marking and movement tracking on the radar to characterize vessel abundance, type and position at the beginning and end of each breathing sequence. The position of our research vessel was logged automatically every 10 s using a Global Positioning System, and was used to calculate the whale position from estimated angle and relative distance. This information was then combined with radar-estimated positions of vessels to calculate the distance separating the nearest vessel from the whale at the beginning and end of each breathing sequence. It was assumed that errors in estimated distances were small relative to the defined distance categories.

Blue whales normally structure their surfacings into discrete bouts, with several shorter inter-breath intervals followed by a longer dive. Surface time was defined as the interval between the first and last breath; surface-feeding events not associated with a breath were considered as being part of dive time. Ensuring detection of the whale's first breath can be challenging, but is crucial for accurate behavioural measurement. To increase the probability of first-breath de-

tection, we had 4 observers on the research vessel, each actively scanning and listening for the breath acoustic cue. Sudden movement of whale-watching vessels (when present) in the same direction was used as an additional detection cue. Surface sequences were discarded when whales were only detected due to sudden movement of whale-watching boats. Identification of the last breath of each sequence was facilitated by the tendency of blue whales to arch their back as they dive, showing their dorsal fin and, in some cases, the fluke. These cues, combined with an inter-breath interval several times longer than the previous ones, confirmed the end of the breathing sequence. In certain cases, such as when blue whales engaged in near-surface feeding and dove for short intervals, the end time of a breathing sequence was difficult to identify. Manual validation of surface times was made *a posteriori* by examining inter-breath interval variability. For breathing sequences where start and end times were unambiguously determined by field observers, i.e. usually for sequences of several breaths following dives of several minutes, inter-breath interval averaged 14 ± 6 s (mean \pm SD), with a maximum of 50 s. This maximum value was used to identify termination of a breathing sequence in cases where breaths were taken more irregularly.

Follows were discarded when they were suspected to comprise more than 1 individual. Among the remaining follows, only those with complete data for at least 5 breathing sequences regardless of whether vessels were present or not were retained for analyses. Response variables used to describe blue whale behaviour included surface time (time between first and last breath), inter-breath interval, number of breaths and duration of the following dive. By definition, breathing sequences comprising only 1 breath were missing surface time and inter-breath interval. However, it was possible to estimate surface time for these single-breath sequences using a separate dataset of 10 blue whales also exposed to whale-watching activity in the same area in the early 2000s (Doniol-Valcroze et al. 2011). These whales had been equipped with archival tags that sampled depth (± 0.25 m) every 1 s. Based on 6668 dives and associated surface times (defined as the time spent within 1 m of the surface), surface time for single breath averaged 6 ± 2 s.

Successive measures obtained from focal-followed individual whales are auto-correlated and considered pseudo-replicates. Failing to account for non-independence of model residuals and autocorrelation generally results in underestimated uncertainty of model estimates. Both mixed-effect models and generalized estimating equation (GEE) can fit models to longitudinal/clustered data which include correlated responses (Liang & Zeger 1986, Fieberg et al. 2009). Mixed-effect models are better suited for situations where heterogeneity in individual response is expected as a result of unmeasured factors, whereas GEEs are preferred when the population-averaged response is of primary interest. In the latter case, the distributional properties of the subjects are not included in the estimate of the main response, which depends exclusively on the covariates and not on the random effects (Zuur et al. 2009).

In the present study, 2 specific effects on whale behaviour were of interest: (1) vessel presence within 2000 m of focal whales and (2) distance of the nearest vessel to the whale. A mixed-effects model was the logical choice for examining these effects since factors such as diving depth and behaviour (e.g. transit vs. foraging) were not measured in our study, and likely influenced blue whale surface and dive times (Doniol-Valcroze et al. 2011). A generalized linear mixed model (GLMM) with a Gaussian error distribution and an identity link function was used to model blue whale response to the presence of vessels. The focal individual was included as a random effect. Eighteen follows comprising at least 8 breathing sequences in total, and at least 4 breathing

sequences for each of the 2 treatments (with and without vessels within 2000 m) were included in the analysis. While it is plausible that some individuals were followed more than once during the study, there is no means to verify this given our remote position during follows; therefore, follows were assumed independent. Likelihood ratio tests comparing the null model with the model including vessel presence as a fixed effect were used to validate *t*-test results.

The effect of vessel distance on whale behaviour could not be examined using a GLMM approach due to the lack of individual behavioural data across all distance categories. A GEE–GLM approach was therefore adopted to account for autocorrelation in responses of individual whales, with the caveat that this method provides only population-averaged parameter estimates for each distance category, i.e. it does not account for potential effects of behaviour and foraging depth on responses from individual whales (Wedderburn 1974). The GEE approach also assumes independence among clusters, i.e. the distance categories of individual whales. However, we strongly suspected non-independence among clusters, since whales exhibiting a strong response toward distant vessels were also likely to respond strongly at closer distances, or a whale not responding to a vessel at 400 m was also unlikely to respond to vessels located further away. To comply with the cluster independence assumption, the 11 whales unexposed to vessels were included as independent clusters representing the '2000 m +' distance category, and the 22 whales exposed to vessels at <2000 m were each made an independent cluster by selecting observations only for the distance category with the highest sample size. Since the correlation structure for the errors within each cluster was uncertain, a working independence model was applied as it is preferred over the specification of a correlation structure in such cases (Pan 2001, Fieberg et al. 2009). This approach generally leads to efficient model coefficients and uses robust sandwich estimators to produce realistic standard errors. To ensure that the selected correlation structure was adequate, we repeated the analysis assuming an 'exchangeable' correlation structure, i.e. we assumed within-subject observations were equally correlated. Model selection was based on quasi-likelihood under the independence criterion (QIC). This is an extension of Akaike's information criterion (AIC) that allows the comparison of covariance matrices under GEE models to the covariance matrix generated from a model that assumes no correlation within clusters (Pan 2001). The lower the QIC value, the more appropriate the correlation structure

used to fit the data. Model adequacy was assessed based on a Wald-Wolfowitz run test for randomness of residuals (Chang 2000), and a scale parameter for dispersion (Zuur et al. 2009). Repeated Wald tests were carried out to assess the significance of distance categories, using the 0 to 400 m distance category as a reference (Hardin & Hilbe 2003).

We also assessed whether blue whales were more responsive to the relative distance of a vessel at the start or at the end of a breathing sequence. The relationship between distance of the whale to the nearest vessel (measured by radar, a continuous variable) and each of the response variables was examined using GEE-GLMs. Separate analyses were conducted for response variables at the start and end of a breathing sequence, ensuring independency among clusters. Wald tests were carried out on each model to evaluate covariate significance.

Statistical analyses were performed using the R software (version 3.3.0; R Development Core Team 2008), and the contributed packages 'geepack' v.1.2-0 (Højsgaard et al. 2006), 'adehabitat' v.1.8-18 (Calenge 2006), and 'lme4' v.1.1-12 (Bates et al. 2015). Unless otherwise noted, average results are presented \pm SD.

RESULTS

A total of 43 blue whale encounters and 131 h of observation were made in 2006 and 2010 (31 encounters in 2006 for 34 d of effort and 12 encounters in 2010 over 36 d). In all, 33 focal follows and 106 h of data qualified for analysis. The average duration of focal follow was 3.25 h (range: 0.5 to 10.75 h). Whales spent on average $17 \pm 4.4\%$ ($n = 33$ follows) of their time at the surface.

Vessels occurred <2000 m from focal whales in 23 (70%) of the follows, 91% of which were whale-watching vessels. Exposure to vessels varied among whales from 5 to 100% of observation time, and averaged $59 \pm 31\%$. A maximum of 8 vessels were observed simultaneously within 400 m from blue whales, or 16 vessels when considering radiuses of 1000 or 2000 m. However, median values of 1 ± 1.2 vessels within 400 m ($n = 224$), 1 ± 1.6 vessels within 1000 m ($n = 317$), and 2 ± 1.6 vessels within 2000 m ($n = 395$) indicate that the number of vessels around whales was generally low. However, large variances around mean

estimates (Table 1) indicate that larger aggregations of vessels around whales were not rare.

Vessels affected blue whale diving patterns when present at distances <2000 m. Significant reductions in surface time, dive time and number of breaths per breathing sequence were documented compared to when vessels were absent or at distances >2000 m (Table 2). Examining surface and dive parameters by distance category using the 33 follows as independent clusters revealed that response variables were each best modelled (i.e. had lower QICs) using GEEs that assumed an 'independence' correlation structure among residuals (data not shown); only results from these models are presented. The effect of vessel distance on whale behavioural response was significant for surface time and number of blows (GEE-GLM, Wald test, $p < 0.05$), marginally insignificant for dive time ($p = 0.07$), and not significant for inter-breath interval ($p > 0.05$) and increased with vessel proximity (Fig. 2). In general, it was only once vessels were within 400 m of a whale that response variables became significantly different compared to when no vessels were present within 2000 m of the whales (Fig. 2). At distances <400 m, surface and dive times were on average 49 and 36% shorter, respectively, with a 51% reduction in the number of breaths. These paired comparisons were statistically significant for surface time and number of breaths (Wald tests, all $p \leq 0.05$), and marginally insignificant for dive time (Wald test, $p = 0.059$).

The relative nearest-vessel distance to a whale at the start of a breathing sequence also had a significant effect on all response variables (GEE-GLM, $n = 23$ clusters or whales; Wald statistic, $\chi^2 = 5.3$ to 8.5, all $p \leq 0.02$) except inter-breath interval ($\chi^2 = 0.11$, $p =$

Table 1. Effects of vessel presence within 2000 m of blue whales *Balaenoptera musculus* in the St. Lawrence Estuary ($n = 18$) on various behavioural parameters estimated using generalized linear mixed models (GLMMs) with focal individual as a random effect. The effect of the predictor (vessel presence or absence) on each response variable is expressed using coefficient estimates (β), standard error SE (β), t -value and significance level (p ; t -test using Satterthwaite approximation for degrees of freedom)

Response variable	Predictor	Coef. (β)	SE (β)	t -value	p
Surface time	Intercept	1.26	0.15	8.3	0.0001
	Vessel effect	-0.18	0.04	-4.0	0.0001
Dive time	Intercept	7.28	0.88	8.2	0.0001
	Vessel effect	-0.41	0.19	-2.2	0.029
Inter-breath interval	Intercept	0.23	0.01	26.9	0.0001
	Vessel effect	-0.01	0.01	-1.53	0.13
Number of breaths	Intercept	5.50	0.68	8.07	0.0001
	Vessel effect	-0.60	0.16	-3.79	0.0001

Table 2. Parameters used to evaluate the effect of reducing mean surface and dive times on the time available for foraging by blue whales *Balaenoptera musculus* in a food patch located at depths varying from 1 to 150 m, and calculated for a single dive (F_t) and for a 1 h foraging bout (F_{tot}). F_t and F_{tot} over the 1 to 150 m depth range are presented in Fig. 3. Values provided for dive time and surface time were obtained using a generalized estimating equations for generalized linear model type of data (GEE–GLM) approach and the 33 follows as independent clusters (Fig. 2)

Parameter	Definition	Value if distance to nearest vessel		Change (%)
		>2000 m	≤400 m	
D_t	Observed dive time (min)	6.37	4.05	–36
S_t	Observed surface time (min)	1.25	0.64	–49
DC	Observed dive cycle time (min) ($D_t + S_t$)	7.62	4.69	–38
N_{dives}	Number of dives over 1 h ($60 / DC$)	7.87	12.8	38
V	Transit speed (1 m s^{-1} or 1.5 m s^{-1})			
T_t	Transit time ($2 \times \text{depth} / V$)			
F_t	Time left for foraging ($D_t - T_t$)			
F_{tot}	Total time (min) for foraging over 1 h ($F_t \times N_{dives}$)			

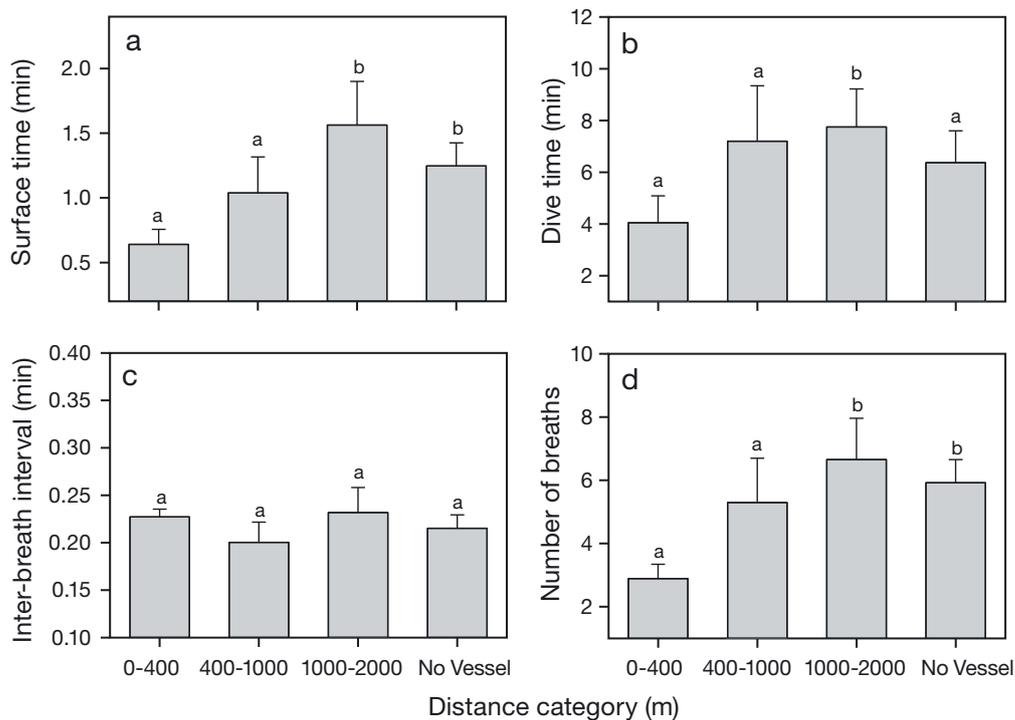


Fig. 2. Effect of vessel distance to blue whales *Balaenoptera musculus*: mean (\pm SE) (a) surface time, (b) post-exposure dive time, (c) inter-breath interval and (d) number of breaths per breathing sequence, assessed using generalized estimating equations with independence correlation structure. Comparisons among distance categories are relative to the 0 to 400 m category. Identical letters above bars indicate lack of significant difference (Wald tests, $p > 0.05$)

0.74). However, no significant relationship was detected when considering the relative nearest-vessel distance to a whale at the end of a breathing sequence (GEE–GLM, $n = 23$ clusters; $\chi^2 = 0.05$ to 2.6, all $p > 0.05$), indicating that blue whale behavioural response to a vessel was driven by the relative proximity of the vessel at the time of surfacing, not at the time of diving.

DISCUSSION

For air-breathing animals living in aquatic environments, an event that reduces time spent at the surface and the number of breaths taken can limit diving capacity, and therefore, foraging time. Because oxygen is acquired at the surface with diminishing returns, recovery times increase rapidly with leng-

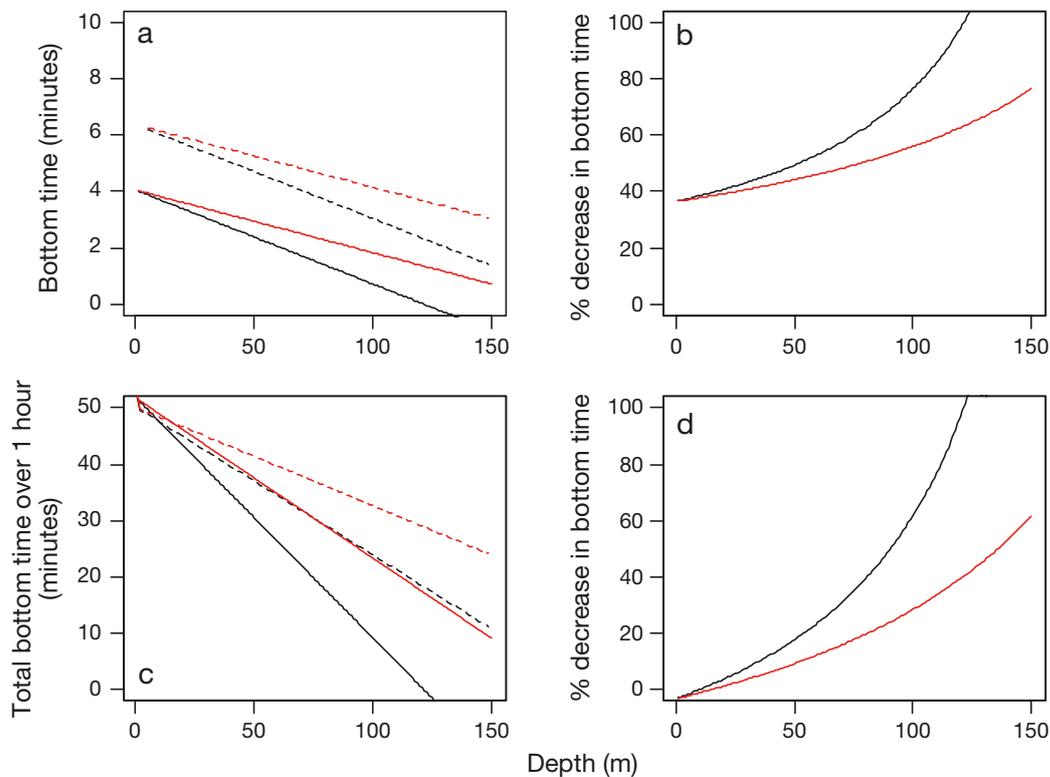


Fig. 3. Change in time available for blue whale *Balaenoptera musculus* foraging (foraging time) as a function of depth during (a,b) single dives and (c,d) a 1 h foraging bout (foraging time per bout), when vessels were present within 400 m of whales (solid line) and when vessels were absent within a 2000 m radius (dashed line). Change in time available for foraging is expressed as absolute time in (a) and (c), and as percent decrease in (b) and (d), as a result of vessel presence when considering the average transit speed (1 m s^{-1} ; black line) and maximum transit speed (1.5 m s^{-1} ; red line) of blue whales

thening of dives (Kramer 1988, Kooyman & Ponganis 1998). Thus, the effects of disrupting surface behaviour may be exacerbated in cases where animals need prolonged at-surface recovery time to perform long or deep dives to reach and efficiently exploit food patches (Thompson & Fedak 2001). This is exemplified in sperm whales, a deep- and long-diving species that consequently requires long recovery times at the surface, and for which a 17% reduction in surface time is estimated to induce a 36% reduction in foraging time (Gordon et al. 1992).

St. Lawrence Estuary blue whales usually forage at greater depths during the day than at night, although near-surface foraging can occur during the daytime (Doniol-Valcroze et al. 2011). Whale-watching activities operate exclusively during the day, when blue whale dives are likely the deepest and recovery times at the surface are the longest. Blue whales employ a relatively costly foraging strategy called lunge feeding (Acevedo-Gutiérrez et al. 2002, Goldbogen et al. 2012). This foraging tactic might lead to shorter than expected dive times (Croll et al. 2001) and regular exhaustion of oxygen stores, placing additional con-

straints on surface recovery time (Potvin et al. 2012). In St. Lawrence Estuary blue whales, optimal dive time and theoretical aerobic dive limit (TADL) converge with increasing depth, because for deeper dives (generally during daytime) a greater amount of time is spent travelling through the water column, thereby constricting time and oxygen stores left available for foraging at depth (Doniol-Valcroze et al. 2011). How often blue whales in the St. Lawrence Estuary rely on anaerobic metabolism as a result of exceeding their TADL is unknown. An oxygen debt can be accumulated over a few dives and repaid later, e.g. at the end of a foraging bout, as observed in some otariids (e.g. Fahlman et al. 2008). However, in the present study, the reduction in dive duration was observed immediately following vessel exposure, suggesting that disruption of breathing sequences and associated reduction in the number of breaths taken has an immediate consequence on dive duration in blue whales.

Blue whales in the St. Lawrence Estuary spend on average $68 \pm 14\%$ of their time foraging during summer (T. Doniol-Valcroze & V. Lesage unpubl. data).

Foraging is thus their primary activity. This implies that the observed reduction in dive time translates to foraging time in most of the blue whales followed, and may result in lost foraging opportunities. The 36% reduction in dive time documented when vessels were within 400 m of whales likely meant a greater than 36% reduction in foraging time for 2 reasons: first, foraging depth is dictated by where krill densities are located. Thus, foraging depth likely remains constant during a foraging bout (i.e. whales cannot choose a different foraging depth to compensate for reduced dive times). Second, a relatively fixed amount of time is needed to reach the preferred foraging depth and food patch. Given that surface time was also shorter in disturbed whales, one could argue that blue whales can compensate for shorter foraging time during a dive by performing more dives during a feeding bout. However, this would entail proportionally more time spent in transit, and hence higher energy expenditure. Blue whales could also increase their transit speed to increase time spent at depth, although this could ultimately decrease net energy gain from foraging by increasing cost of transport.

The effect of changing transit speed or increasing diving rate on foraging time can be explored using dive duration and surface time documented in presence and absence of vessels, while making no assumption about optimality or target foraging depth. Transit speeds have been estimated for blue whales, and average 1 m s^{-1} with maxima of around 1.5 m s^{-1} (Doniol-Valcroze et al. 2011, Goldbogen et al. 2011, McKenna et al. 2015). Let us first consider scenarios where transit speed is unaltered by vessel exposure, and fixed at 1 m s^{-1} . When accounting for transit time to reach a given depth varying between 1 and 150 m, time available for foraging during single dives decreases linearly with depth, and is consistently shorter when vessels are present within 400 m of blue whales than when they are absent from a 2000 m radius around them (Fig. 3a). Based on our results, whales that are not exposed to vessels can reach food patches located at 150 m or deeper and still have time to forage to some extent, whereas whales within 400 m of vessels have no time left to forage at depths beyond 121 m (Fig. 3a). The relative proportion of lost foraging time as a result of vessel exposure (<400 m) increases exponentially with depth (Fig. 3b). Although shorter dive times and surface sequences allow for an increased diving rate, the effective foraging time remains a function of the overall time spent at depth foraging during the entire bout. For a 1 h foraging bout, and assuming transit speed is con-

stant at 1 m s^{-1} , a total of 7.9 dive cycles (surface + dive time) are performed on average in the absence of vessels. This number could theoretically almost double to 12.8 dive cycles h^{-1} if blue whales increased their diving rate in response to vessels within 400 m (Table 2). However, given that transit time is a fixed component for each dive, time available for foraging in a food patch still decreases with depth when integrated over a 1 h foraging bout, except when blue whales are surface-feeding (Fig. 3c). For instance, for a blue whale feeding at a 10 m depth or less, the decrease in foraging time per dive can theoretically be fully compensated by increasing the number of dives performed during the 1 h foraging bout, for a possible total increase in foraging time of up to 3% (Fig. 3c). However, at greater depth, foraging time lost during individual dives cannot be fully compensated by increasing diving rate. Increasing transit speed to 1.5 m s^{-1} increases depth at which full compensation is possible to 15 m (Fig. 3a). While some blue whales forage at these shallow depths during daytime in the St. Lawrence Estuary, the majority of individuals target deeper food patches, generally between 30 and 100 m, with a maximum foraging depth documented at 128 m (Doniol-Valcroze et al. 2011).

We showed that even if blue whales increase transit speed and diving rate, they cannot compensate for shorter dive time over most of the range of targeted depths. A meta-analysis has documented cetacean response to whale-watching and indicates that a shift in activity budget towards decreased foraging and resting times is a fairly consistent response to vessel exposure across cetaceans, including blue whales (Senigaglia et al. 2016). For instance, fin whales *Balaenoptera physalus* foraging off the coast of Maine, USA, in proximity to whale-watching vessels decreased their surface time and number of breaths by 9 and 10%, respectively, and their dive duration by 14% (Stone et al. 1992). Icelandic minke whales *Balaenoptera acutorostrata* also interrupted their foraging activity in addition to reducing their inter-breath interval as a result of exposure to whale-watching vessels (Christiansen et al. 2013a). Documented responses of blue whales exposed to vessels or mid-frequency military sonars also suggest that they are unlikely to increase diving rates or swim speed as compensatory strategies to maintain foraging time (Goldbogen et al. 2013, McKenna et al. 2015). Blue whales decreased deep-foraging when exposed to military sonars, whereas they tended to perform 'response dives' when exposed to collision risks (McKenna et al. 2015). Response dives are typically

shallow (<30 m), involve no foraging (no lunges) and have slower descent rates compared to 'undisturbed' foraging dives. Some of the dives following vessel exposure in our study might have been response dives. Unless food patches were located within 30 m of the surface, response dives likely represented a full loss of foraging time given that blue whales were unable to reach feeding depth.

A possible effect of our research vessel on the behaviour of blue whales cannot be excluded. However, we considered this effect to be relatively constant and unlikely to bias our results given that the distance of our vessel to the whale (which varied from 400 to 800 m) invariably fell into a single 400 to 1000 m distance category we set, and was outside that of closest vessel proximity to whales (i.e. ≤ 400 m), where the most significant behavioural changes were documented. Moreover, our vessel was not moving during blue whale surface sequences, to further minimize disturbance.

Being the largest animals on Earth with a highly specialized diet (stenophagous), blue whales have the greatest absolute metabolic demands, and their foraging behaviour is strongly driven by the availability and depth of dense krill patches (Goldbogen et al. 2015). As a result, they are particularly vulnerable to changes in prey abundance or distribution, or prey access (Croll et al. 1998, Clapham et al. 1999, Acevedo-Gutiérrez et al. 2002). Repeated disturbance can reduce prey access and overall foraging success by limiting dive time if oxygen stores cannot be adequately replenished at the surface, or can force whales to move to areas of sub-optimal quality with less dense or less accessible patches of krill. Disruption of breathing sequence and thus impairment of oxygen replenishment over short periods of time may possibly be compensated by increased feeding rates at a later time, as proposed for some odontocete species (e.g. New et al. 2013). The likelihood of effects on the fitness of individuals depends on their ability to compensate and varies according to specific ecological and social conditions (New et al. 2013). In true capital breeders such as Balaenopteridae, the degree of flexibility to cope with foraging disruption may not be as large as in small odontocetes. In Icelandic minke whales, blubber volume increases linearly over the feeding season (Christiansen et al. 2013c), suggesting that their aim is to put on as much fat as possible during the feeding season to complete their annual cycle. Blue whales likely have limited flexibility in coping with repeated foraging disruption given that foraging already constitutes a large proportion of their activity budget in the St. Lawrence Estuary.

The majority of blue whales encountered in this study were exposed to whale-watching vessels, which were present during more than half of the observation period on average. Given the intense whale-watching activity, small territory and low number of individuals present in the St. Lawrence Estuary at any given time (usually less than 8 or 10), each blue whale is exposed possibly daily and for several hours a day to this activity during their summer feeding season. Effects of whale-watching activities on surface and diving patterns were particularly notable when vessels occurred within 400 m of the whales, but were perceptible when vessels were at distances up to 1000 m. Behavioural responses of blue whales in this study were of a larger magnitude compared to those documented in fin and minke whales from other areas (Stone et al. 1992, Christiansen et al. 2013a), suggesting that this population might be particularly sensitive to disruptive activities when animals are foraging. Recent reviews of behavioural responses of marine mammals to various sources of anthropogenic noise and activity have concluded that behavioural response is highly context-specific (Gill et al. 2001, Southall et al. 2007, Ellison et al. 2012, Gomez et al. 2016). There is a need to investigate whether foraging depth and frequency of exposure to vessels affect the behavioural response of blue whales (Laist et al. 2001, Goldbogen et al. 2013). A larger sample size would have allowed some of these effects to be explored, as well as other contextual aspects such as the effect of vessel speed or angle of movement relative to the whale, vessel type, abundance and configuration around the whale. Nonetheless, our results indicate that preventing vessels from entering within a 400 m radius around blue whales can help reduce the negative effects of marine recreational activities on foraging blue whales. This exclusion zone, which is currently in place in the Saguenay-St. Lawrence Marine Park, could be extended elsewhere.

A direct assessment of the impact of whale-watching on foraging success was not possible in this study. However, considering the intensity of whale-watching activities in the region and of the dive time reductions documented in this study, it is warranted to proceed with a study of the cumulative effects of chronic exposure to vessels on vital rates of blue whales (e.g. New et al. 2013, 2014, Christiansen & Lusseau 2015, Christiansen et al. 2015, King et al. 2015). The application of such models to St. Lawrence Estuary blue whales would help determine the threshold beyond which whale-watching or other marine recreational activities may reduce fitness and have population-level effects.

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