

Stimulus-dependent response to disturbance affecting the activity of killer whales

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Abstract

Humans seeking to observe wildlife in their natural habitat can disrupt the activity of the individuals they target. One hypothesis is that behavioral reactions emerge from animals perceiving humans as a potential risk. If it was the case we expect the avoidance tactics to be mediated to account for the difference in risk factors different platforms might present. We examined whether behavioral responses of northern resident killer whales differed between powerboats and kayaks to test this prediction. Killer whales responded to kayaks by increasing their probability to switch to travelling activity more often than during control (no-boat) conditions. As a result, killer whales spent significantly more time traveling when in the presence of kayaks than they did under control, no-boat conditions (11% increase in time spent travelling). Consistent with previous studies examining the effects of powerboats, killer whales significantly reduced overall time spent feeding in the presence of kayaks and powerboats (30% decrease in the time spent feeding). Overall, we show that killer whales have different avoidance tactics to deal with the two types of vessels (motorized or not) and that they will try to outpace kayaks because those cannot follow them. The presence of motorized vessels, particularly vessels targeting whales, decreased the odds that killer whales were feeding (odds ratio: 0.70, 95% CI: 0.62-0.79). The presence of kayaks increased the odds that killer whales were traveling (odds ratio: 1.13, 95% CI: 1.001-1.280). Silent vessels (kayaks) can therefore elicit avoidance tactics like boats that have an acoustic signature do. Such findings are consistent with observed risk avoidance strategies in long-lived mammals. These avoidance strategies have different energetic consequences. While both kayaks and powerboats affect both feeding and travelling behavior, kayaks tend to increase killer whales' energetic demand while powerboats tend to decrease their opportunities to acquire energy.

Introduction

Boat traffic has been shown to affect the short-term behavior (Williams et al. 2002a, b; Williams and Ashe 2007; Noren et al. 2009; Williams et al. 2009a) and activity budgets – including feeding activities (Williams et al. 2006; Lusseau et al. 2009) – of northern and southern resident killer whales. Periods of reduced prey availability have been linked to periods of high adult mortality (Ford et al. 2010) and reduced reproduction (Ward et al. 2009) in resident killer whales. As a result, the potential for boat traffic to reduce feeding activity has been identified as a causal factor in the endangered status of resident killer whales. Vessel traffic has been a priority topic for research and management, in part because it is among the most tractable risk factors to deal with in the short term. Boat-based disturbance can be mitigated through whalewatching guidelines¹, and through the creation of no-entry marine protected areas (Williams et al. 2009b; Ashe et al. 2010).

A proposed, “No-go” marine protected area (MPA) for southern resident killer whales (SRKWs), has triggered a round of discussion about which vessel types, if any, should be exempt from the no-entry policy. One school of thought suggests that kayaks should be allowed to enter the MPA, because they are essentially quiet underwater. Indeed, it has been almost taken as given that noise is the stimulus that is causing the observed behavioral responses – a suspicion that has been borne out by several lines of research. In the case of evasive tactics, it has been shown experimentally that the magnitude of avoidance responses was higher to a louder boat (Williams et al. 2002b) than to a quieter one (Williams et al. 2002a). Secondly, avoidance response was stronger as boats approached whales more closely (and received noise level tends to increase) (Williams et al. 2002a; Williams et al. 2009a). Third, the observed evasive tactic changed as the number of vessel increased to three or more vessels (Williams and Ashe 2007). In each of these studies, non-motorized vessels including kayaks were included in boat counts. In the case of acoustic response to vessel noise, killer whales have responded by increasing the amplitude (Holt et al. 2004) and length (Foote et al. 2004) of social calls.

But the suspicion of a dose-response relationship between received noise level and the strength of the evasive response is simply that, a suspicion. The potential for masking of social calls, temporary and permanent hearing loss and behavioral responses over ranges of vessel noise have been modeled (Bain and Dahlheim 1994, Erbe 2002). At extreme amplitudes, acoustic disturbance has been linked with habitat displacement in northern resident killer whales (Morton and Symmonds, 2002).

Anecdotally, people have referred to kayaks as potentially eliciting a startle response from killer whales. To the best of our knowledge, no scientific studies have formally evaluated whether killer whales evade kayaks, although voluntary guidelines have been adopted

¹ <http://www.bewhalewise.org/bewhalewise.pdf>

locally to manage kayaking around SRKWs². Bottlenose dolphins (*Tursiops truncatus*) engaged in foraging activity have been observed evading kayaks by repeatedly swimming up to 200m away from approaching kayaks (Gregory and Rowden, 2001). Studies in Fiordland, New Zealand also should that kayaks could elicit the same avoidance responses as powerboats could by bottlenose dolphins (Lusseau 2003a, 2006). Henry and Hammill (2001) note that the behavioral response to disturbance among hauled-out harbor seals was “most-severe” with kayaks relative to other sources of disturbance, such as motorized vessels and sailing vessels.

It would be difficult to conduct control-exposure experiments on SRKWs to measure responses to kayaks. Opportunities to view SRKWs in the absence of boats, let alone to manipulate boat traffic near focal animals under controlled conditions, are rare (Williams et al. 2009a). Of course, the fact that no studies have explored this topic is one of the best reasons to ensure that a “boat-free” MPA is applied equally to all vessel types. This would allow researchers to view whales in the absence of boats, then experimentally manipulate boat traffic of different vessel types, and measure the response. This approach has been successful in Robson Bight (Michael Bigg) Ecological Reserve (RBMBER) (Williams et al. 2002a, 2002b; Williams and Ashe 2007). The precautionary principle would strongly suggest that an MPA should apply to all vessels until evidence is available to give any vessel type an exemption.

In the meantime, data exist to evaluate whether behavioral responses of northern resident killer whales (NRKWs) differed between powerboats and kayaks. The NRKW population was used previously as a proxy for SRKWs when it was unfeasible to conduct multiple-vessel experiments around the latter (Williams and Ashe 2007). While it is not ideal to rely on a proxy population, it does represent an efficient, cost-effective and pragmatic approach to generate hypotheses to be tested on SRKWs. In order to make the proxy as relevant to SRKW conservation and management as possible, it should be noted that we are working with the same species, on a population that is closely related genetically, shares a similar diet, uses adjacent habitat (geographically) (Ford et al. 2000). One of the key biological differences between the two populations is cultural, namely the fact that NRKWs rub on beaches, while SRKWs do not (Ford et al. 2000); as a result, we conducted analyses with and without beachrubbing activities to facilitate between-population comparisons. The use of proxies should not be considered solely a drawback. In any science ethics review, it would always be considered precautionary to use the least invasive method possible, and to use suitable proxies in lieu of experimenting on endangered species.

Notwithstanding the management applications, understanding how killer whales react to different boat stimuli can inform the way the animals may perceive boat disturbances. One school of thought is that disturbance is perceived as pseudo-predation risk. It could be that behavioral response follows a classic dose-response curve driven entirely by received noise

² http://www.whalemuseum.org/images/misc/KELP_Code_Poster.gif

level. Or there may be other behavioral mechanisms at play. The key question remains: Do killer whales show behavioral responses to quiet boats?

Methods

FIELD SAMPLING AND DATA HANDLING

Field methods and original data analysis methods have been described previously (Williams et al. 2006). Data were collected from a cliff on West Cracroft Island (Fig. 1) approximately 50m above mean water level, which offered an expansive view of Johnstone Strait and RBMBER. The RBMBER is a voluntary 'no-go' zone kept largely free from boats by a seasonal warden, boater-education program. Field seasons varied in length among years (1995–2004). A minimum of three observers recorded boat and whale activity from 08h00 to 20h00 daily. The study area was divided into eight zones, four inside RBMBER and four in the waters immediately adjacent to RBMBER. These zones were readily identifiable from the cliff based on sightlines drawn to prominent landmarks. Every 15 min, observers scanned the area with 7 X 50 binoculars and a 25 X 50 spotting scope to record the number of boats of each vessel type (including non-motorized vessels) in each zone of the study area.

Whale activity was recorded on the same 15-minute schedule by scanning the main activity of whales in focal groups (Altmann, 1974). Whales were recorded as being in a group if they were within approximately 10 body lengths of one another, and displaying the same behavior at the surface. Once whales entered the study area, observers used both visual and acoustic cues to identify matriline and individuals within matriline using photo-identification catalogues (Ford et al., 2000). The exact identification of individuals was not always necessary to follow groups because of the ease of tracking separate schools across sampling periods. Focal groups were defined post-hoc from the subset of the data in which group composition remained constant across a sequence of samples.

Whale activity recorded during each 15-minute scan sample was assigned to one of five mutually exclusive and cumulatively inclusive activity states (Table 1). The definitions of these states were adapted from those used in other killer whale behavior and bioenergetics studies (Felleman et al., 1991; Hoelzel, 1993; Kriete, 1995; Barrett-Lennard et al., 1996; Ford et al., 2000; Lusseau et al., 2004; Ford and Ellis, 2006). At each scan, the whales were recorded as being either inside or outside the reserve, based on zone boundaries. This allowed subsequent accounting for known effect of location on whale behavior (e.g., beach-rubbing). The whale data were collected by a single, experienced observer dedicated to whale data collection, whereas the boat data were collected by a collection of volunteer and paid observers over the years.

Table 1 – List of activity states used in this study

Activity state	Definition
Resting	Whales were swimming at slow speed with highly predictable sequences of several short (30 s) dives followed by a long dive of 3–5 min. This activity state was characterized by the absence of surface-active behavior (e.g., breaching or tail-slapping)
Beach-rubbing	Whale presence within 50 m of a gravel beach; independent surfacing and diving of individuals; long periods spent stationary at the surface, followed by slow swim speeds toward a beach; at which point, bubbles or splashing could be observed in the vicinity of the beach
Traveling /Foraging	Whales surfaced and dove independently but all whales in the group were heading in the same general (east–west) direction. The dive sequences of individuals showed regular patterns of several short dives followed by a long one, and whales swam at moderate speeds
Feeding	Individuals were spread out across the Strait; individuals were surfacing and diving independently in irregular sequences of long and short dives; and individuals displayed fast, non-directional surfacings in the form of frequent directional changes
Socializing	Animals surfaced in tight groups with individuals engaged in tactile behavior; whales showed irregular surfacing and diving sequences and swim speeds; irregular direction of movement; and high rates of surface- active behavior

CONTRASTING GENERALISED LINEAR MODELS OF ACTIVITY COUNT DATA AND MODEL SELECTION CRITERIA

We assessed whether boat type may play a role in the effect of boat interactions on whales' activity states in two ways: (i) considering kayaks as different from other boats, and (ii) considering kayaks as different from other boats in addition to categorizing those other boats as either non-targeting (vessels engaged in activities other than whalewatching) or targeting (vessels that may potentially have been engaged in whalewatching). For each set of analyses we fitted generalized linear models to the activity count data with a Poisson error distribution (Lusseau 2003b). In all null models, activities occurring at time step t (succeeding activity, S) were assumed to be influenced by the activity state of the focal school at time $t-1$ (preceding activity, P). We also assumed interactions between our boat variables (boat presence, B , and/or boat type, T) and the initial activity state (P), in order to account for differing number of samples obtained under these different (activity x boat)

conditions (Lusseau 2003b; Williams et al. 2006). To assess the effects of boat interactions we added additional components to this null model that related to the effects of boats on succeeding activities and on the transition from preceding to succeeding activities (i.e., for example the interaction terms BxS and BxPxS). We tested the statistical significance of these components by comparing the added amount of deviance explained by these more complex models to the deviance that the null model could explain using likelihood ratio test. We assumed the difference in deviance is χ^2 distributed with degrees of freedom (df) which is the difference in dfs between the two contrasted models.

The advantage of our null models, that accounts for the autocorrelation in the activity state time series, is that the resulting transition probability matrices can then be further analyzed to provide a robust inference of the activity budget and the typical duration of an activity bout under different conditions (boat type presence) (Lusseau 2003b). We inferred activity budgets under the three boat type conditions (control, kayak, power vessels) using the eigen-decomposition of the transition probability matrices. The resulting dominant eigenvector for each matrix corresponds to the activity budget under each condition. In addition, typical bout duration can be estimated robustly using the geometric mean of the probability to remain in each state (p_{ii}). We then bootstrapped activity transitions to infer the confidence intervals around the activity budget and activity bout duration. We also used the bootstrap to estimate the likelihood that the difference in time spent in each activity and the duration of activity bouts between treatment levels was greater than zero.

INFERRING THE MARGINAL PROBABILITY TO OBSERVE WHALES IN GIVEN ACTIVITIES DEPENDING ON THE CONDITIONS TO WHICH THEY ARE EXPOSED

We know that activity state data obtained from group focal-follow time series are autocorrelated, and indeed this autocorrelation has been investigated at length here (above) and elsewhere (Lusseau 2003b, Williams et al 2006). It is therefore important to incorporate this temporal autocorrelation structure in any statistical model used to assess the likelihood that an activity was observed. We used generalized estimating equations (GEE) to model the influence of natural factors and boats on the likelihood that an activity was observed in contrast to others (using a binomial distribution for errors and a logit link function). We incorporated an autoregressive correlation structure in the covariance matrix where activity state samples from the same focal follow were depending on the activity observed at the previous time step with a constant correlation parameter (ρ) estimated from fitting the GEE model to the data. We did not investigate different correlation structures, because in this case the correlation structure is informed by biological studies showing that an autoregressive function with a lag of 1 is a biologically appropriate structure for autocorrelation in group focal-follows of this species (Williams et al. 2006). We used GEE because, in contrast to generalized linear mixed effects models (GLMM), they produce unbiased marginal parameter estimates. However, the trade-off is that they cannot

produce conditional estimates for parameters. Conditional estimations are useful in situations where we are interested in subject-specific variability, which in our case would be individual focal follows. However, the central aim of this study is focused on the 'population-averaged' response to covariates, and therefore GEE provides a means to obtain an unbiased estimate of it, whereas GLMM in many cases would not.

GEE models were implemented using the package `geepack` v. 1.0-17 in R 2.12.0 (R Core Development Team 2005). We develop contrasting biological models based on our hypotheses and assessed goodness-of-fit of those models using Pearson's χ^2 statistic (Yan 2001). We first assessed whether activities differed depending on years and months of the study, because previous work showed that whales forage in this area and behaviorally respond to inter-annual variability in Chinook salmon (*Oncorhynchus tshawytscha*) availability (Lusseau et al. 2004). Chinook salmon present in the study area spawn in the Fraser River and therefore the timing of the salmon run influences the monthly variation in salmon availability at our site. School size is also an important contributor to school activity state as killer whales are social cooperative foragers (Ford et al. 2002). Given the natural variability in activity inherent to these covariates, we then assessed the influence of the presence and number of kayaks and motorboats separately and mutually. We used the Quasi-Akaike Information Criterion (QIC, R function in the Supplementary Information) developed for GEEs for model selection (Pan 2001). The theory behind QIC is not as well developed as it is for AIC (Burnham & Anderson 2002), so while the minimum QIC represents the best fitting model, there is no guidance on when others can be disregarded (i.e., there is no rule of thumb based on Δ QIC). Here we assumed that differences of several units represent a significant departure from the best fitting model and we additionally used likelihood ratio tests (Wald's χ^2 statistic) for nested models.

Results

CHANGES IN ACTIVITY STATE DYNAMICS

Boat presence affected the activity in which whales would next engage (Supplementary Information (SI) Table 1), a finding we had previously reported (Williams et al. 2006). When contrasting the effects of boat presence and boat types using 3 categories to describe boats, boat presence alone still emerges as the best predictor for the variance in transition probabilities between activity states (SI Table 2). While boat type has a significant effect on activities, this effect explains less of the variability in activity transition than a simpler effect of boat presence alone (Δ AIC=5, SI Table 2). Hence, consideration of this boat type effect is not warranted. However, when we consider only two boat categories (kayak vs other vessels), we see that the difference between the two models is less pronounced (Δ AIC=1.6, SI Table 3). Hence, we have much less support to discount the boat type model under these

categorization assumptions and we therefore proceeded in comparing activity budget and activity bout durations between these two boat types.

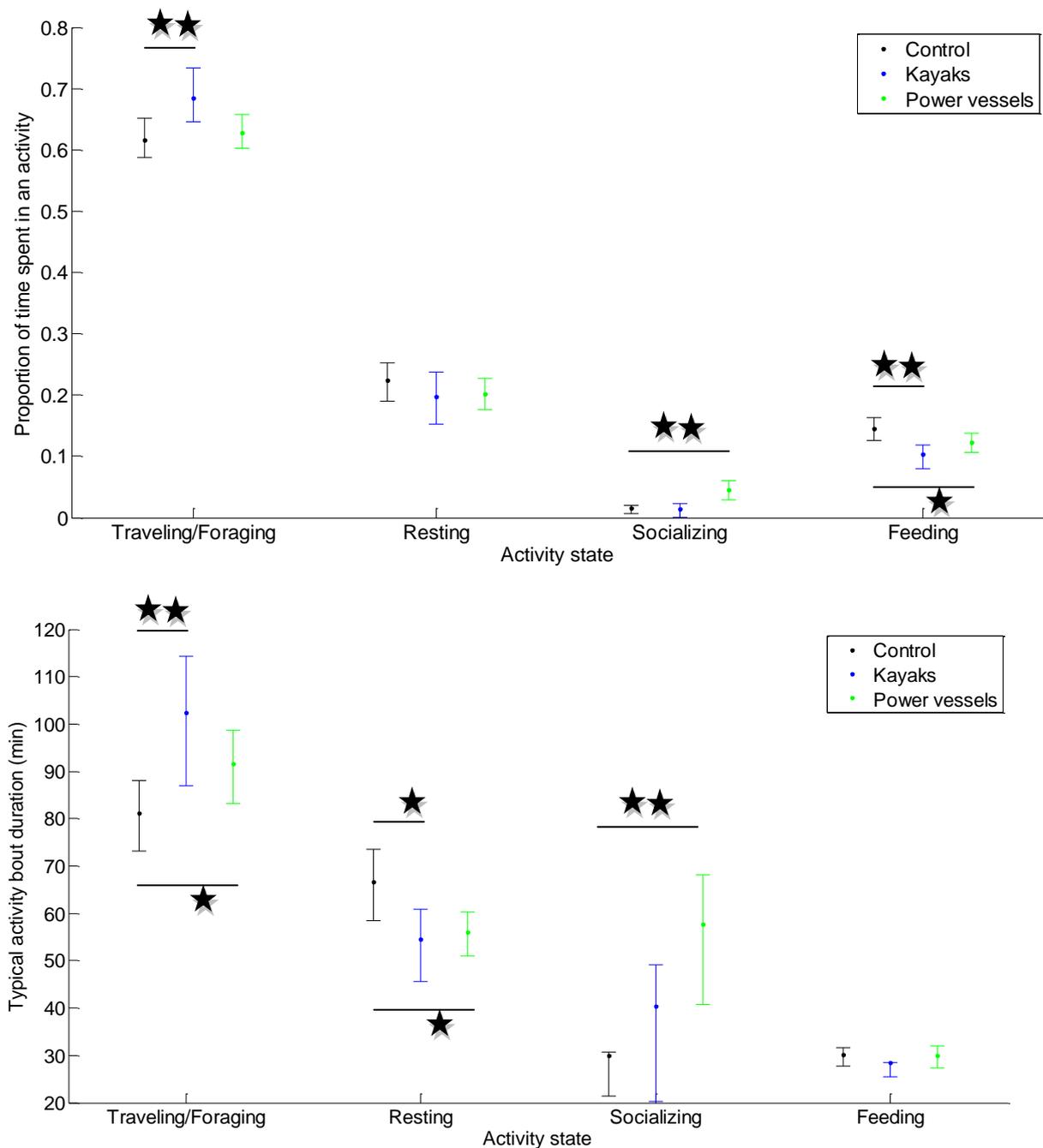


Figure 1. The activity budget (a) and typical activity bout duration (b) of killer whales off the Robson Bight reserve (excluding the area surrounding the rubbing beach) when exposed to the three boat treatments (control, kayak, and other vessels). Error bars are 95% bootstrapped confidence intervals. Pairwise bootstrapped difference, likelihood it is significantly different from zero (0.05-0.01:*, 0.01-0.001:**)

We found some differences in the effects of kayaks and power vessels on activity budgets. The effect on feeding was the same between the two boat types. However, killer whales spent more time traveling when in the presence of kayaks than if kayaks were absent (Figure 1a). This discrepancy in effects is also observable when estimating the typical activity bout duration under the different treatments (Figure 1b).

These results suggest that killer whales have different tactics to deal with different types of vessels. In cases where killer whales are exposed to vessels they may be able to easily outpace (e.g., kayaks), whales engage in horizontal avoidance tactics by switching to or remaining in travel (SI Figure 1). Importantly, the overall effect on feeding activities seems to be similar whether the boats involved are kayaks or other types of vessels. However, kayaks appeared less likely to disrupt a feeding bout (SI Figure 1, $p_{F \rightarrow F}$).

These analyses excluded the zone around the rubbing beach. Previous studies have shown that killer whales use these zones for different purposes and that their activity budget therefore differed depending on the zone (Williams et al. 2006, 2009b). Specifically, northern resident killer whales engage in beach rubbing almost exclusively in zone 6. Southern resident killer whales do not engage in beach-rubbing activities. We wanted our analyses on northern residents to serve as a proxy for southern residents. Consistent with the previous analyses, we found that indeed the effect of vessel type is still present when accounting for focal follows in all zones of the study area (SI Figures 2 & 3).

CHANGES IN THE LIKELIHOOD TO BE IN A GIVEN STATE

Model selection

Given that the aim of this study is an understanding of cost:benefit trade-offs of disturbance under different ecological conditions, we restricted analyses to zones other than zone 6, removing activities surrounding beach rubbing. (Note that we obtained similar results when considering all zones and all activities, but the restricted analyses are more directly interpretable for southern resident killer whales, which do not engage in beach rubbing.) We were particularly interested in the likelihood to observe travelling and feeding under different boat conditions, as those are drivers of the whales' energetic budget (Williams et al. 2006). All fitted GEEs had estimated dispersion parameters, ϕ , close to 1. Models provided good fit to the data (SI Tables 4-8). We did not have collinearity issues. Importantly, the number of kayaks present was not strongly related to the number of power vessels present (Pearson's $\rho=0.29$) and this latter was also not correlated with non-targeting vessel traffic (Pearson's $\rho=0.12$). The likelihood to observe resting and socializing activities were not influenced by boat presence (SI Tables 7 and 8).

Table 2. Generalized Estimating equations model explaining the likelihood to observe feeding in contrast with all other activities (9854 focal follows, maximum focal follow duration 5h30, $\varphi=1.06$, $SE=0.637$; $\rho=0.37$, $SE=0.164$; analysis of Wald's χ^2 statistic table with terms added sequentially). Hereafter we refer to this model as GEE_F.

Effect	χ^2	Df	P
Year	180	9	<0.0001
Month	114	3	<0.0001
School size	152	1	<0.0001
Presence of targeting powerboat	34	1	<0.0001

The best model to explain the likelihood to observe feeding in contrast to other activities included the effect of the presence of targeting powerboats (Table 2). The next best fitting model also included the effect of kayak presence, however this effect did not significantly influence the odds of observing feeding behavior (quasi-likelihood ratio test: Wald=0.75, df=1, p=0.38). In contrast, kayak presence influenced the likelihood to observe whales traveling (SI Table 5). Adding the effect of kayak presence increased the information provided by the model and provided the best fit to the data (Table 3 and quasi-likelihood ratio test: Wald=3.95, df=1, p=0.04). Other models with QIC close to the best model (presence of powerboats, and considering the number of kayaks present) did not improve the fit (quasi-likelihood ratio test all non-significant).

Table 3. Generalized Estimating equations model explaining the likelihood to observe traveling in contrast with all other activities (9854 focal follows, maximum focal follow duration 5h30, $\varphi=1.07$, $SE=0.0194$; $\rho=0.81$, $SE=0.019$; analysis of Wald's χ^2 statistic table with terms added sequentially). Hereafter we refer to this model as GEE_T.

Effect	χ^2	Df	P
Year	58.1	9	<0.0001
Month	41.3	3	<0.0001
School size	25.0	1	<0.0001
Presence of kayaks	3.95	1	0.04

In addition to these contrasts, we also analyzed how covariates influenced the odds of observing feeding instead of traveling (pair-wise contrast of activity states). This analysis was derived from the inferences we made previously of the effects of boat presence on activity transition probabilities. The best fitting models in that case included the effect only of vessels that are likely to be interacting with the whales (powerboats as well as powerboats and kayaks). Importantly, we could not discount a model that included an effect of targeting powerboat number present varying between years (quasi-likelihood ratio test contrasting model with and without interactions: Wald =33.1, df=9, p=0.0001). Since the QIC difference with the better fitting models was very small (SI Table 6) and the best fitting model containing an effect of kayak presence failed to provide more information than

simpler ones (quasi-likelihood test, adding kayak effect: Wald=1.5, df=1, p=0.22), we retained this model to explain the odds of observing feeding instead of traveling (Table 4).

Table 4. Generalized Estimating equations model explaining the likelihood to observe foraging in contrast with traveling (8587 focal follows, maximum focal follow duration 3h30, $\varphi=1.05$, SE=0.249; $\rho=0.39$, SE=0.0725; analysis of Wald's χ^2 statistic table with terms added sequentially). Hereafter we refer to this model as GEE_{FT}.

Effect	χ^2	Df	p
Year	213.2	9	<0.0001
Month	125.2	3	<0.0001
School size	88.1	1	<0.0001
Number of targeting powerboats present	6.9	1	0.009
Year x number of targeting powerboats	33.1	9	0.0001

Model interpretation

When targeting powerboats were present, the odds that killer whales were feeding were decreased (estimated odds ratio for targeting powerboat presence (GEE_F): 0.70, 95% CI: 0.62-0.79, Figure 2). The presence of kayaks increased the odds that killer whales were traveling (estimated odds ratio for targeting powerboat presence (GEE_T): 1.13, 95% CI: 1.001-1.280, Figure 3). These results are consistent with the previous analyses, confirming a difference in the effect of the two vessel types. Interestingly here, we also confirm that whales responded differently to the presence of targeting powerboats compared to other types of vessel traffic.

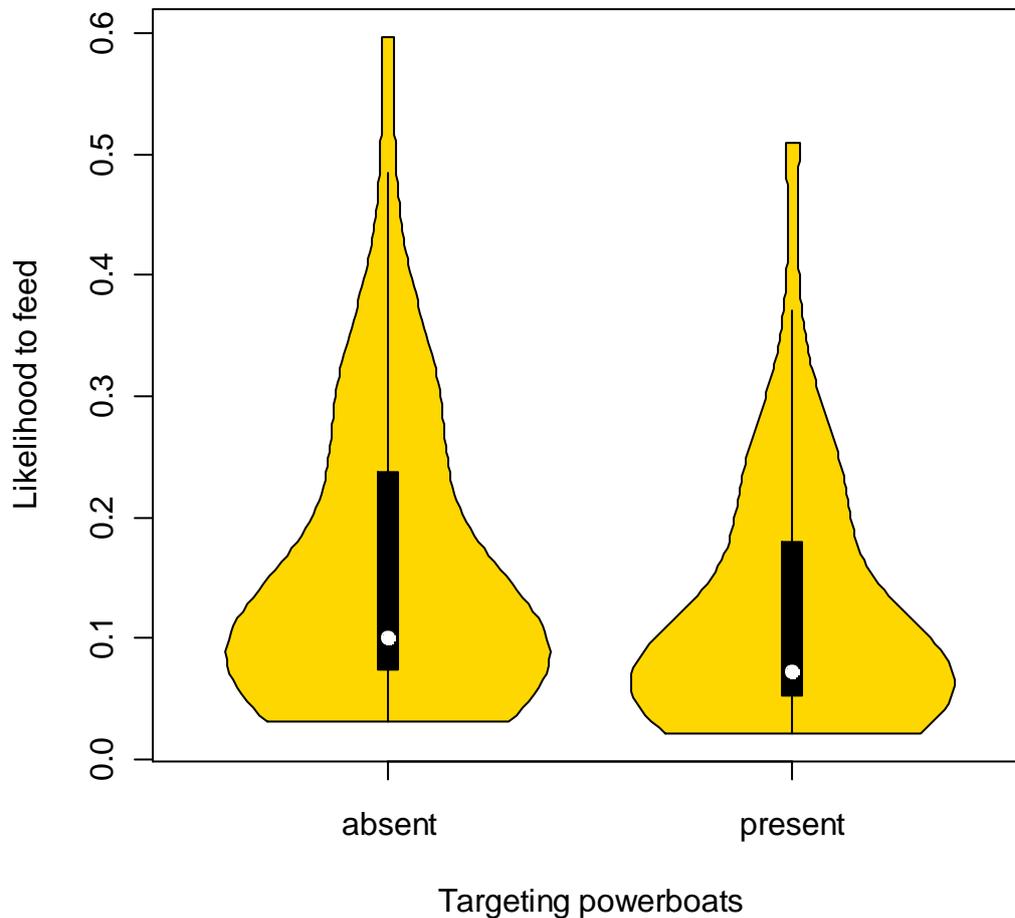


Figure 2. Difference in the predicted probability to observe killer whales feeding depending on the presence of targeting powerboats. A violin plot starts with a box plot, then adds a rotated kernel density plot to each side. The result shows more information on data spread than a boxplot alone, but showing the probability density of the data at different values. A probability density plot is like a histogram in which each block is centred at each data point rather than fixing the end points of the blocks in the form of bins. This approach removes the dependence of the resulting distribution on arbitrary choices in the end points of the bins. The dot in the centre marks for the median value; the black box indicates inter-quartile range; and the outer, irregular shape is the kernel density estimation. This figure shows violin plots (boxplot and kernel density plot combined) of predicted likelihood to feed (GEE_F) with and without boats for a median size school of whale and for all years and all months.

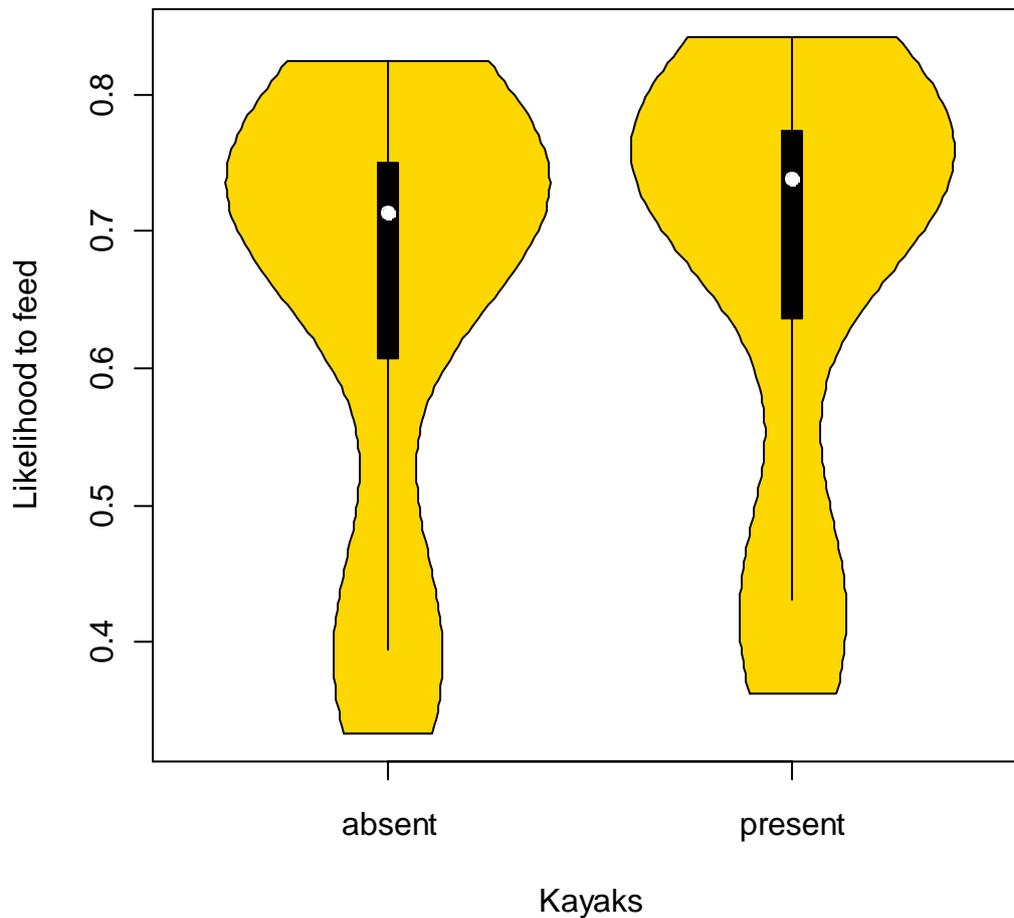


Figure 3. Difference in the predicted probability to observe killer whales traveling depending on the presence of kayaks. Violin plots (boxplot and kernel density plot combined) of predicted likelihood to travel (GEE_T) with and without kayaks for a median size school of whale and for all years and all months.

There was a marked inter-annual variability in the likelihood to observe schools of killer whales feeding at the site (Figure 4a). This variability was correlated to the relative abundance of Chinook salmon, the preferred prey of killer whales in the region (Ford and Ellis 2006; Lusseau et al. 2004) ($\rho=0.76$, randomized $p=0.03$). The observed inter-annual variation in the effect of targeting powerboats is related to this inter-annual variability (Figure 4b).

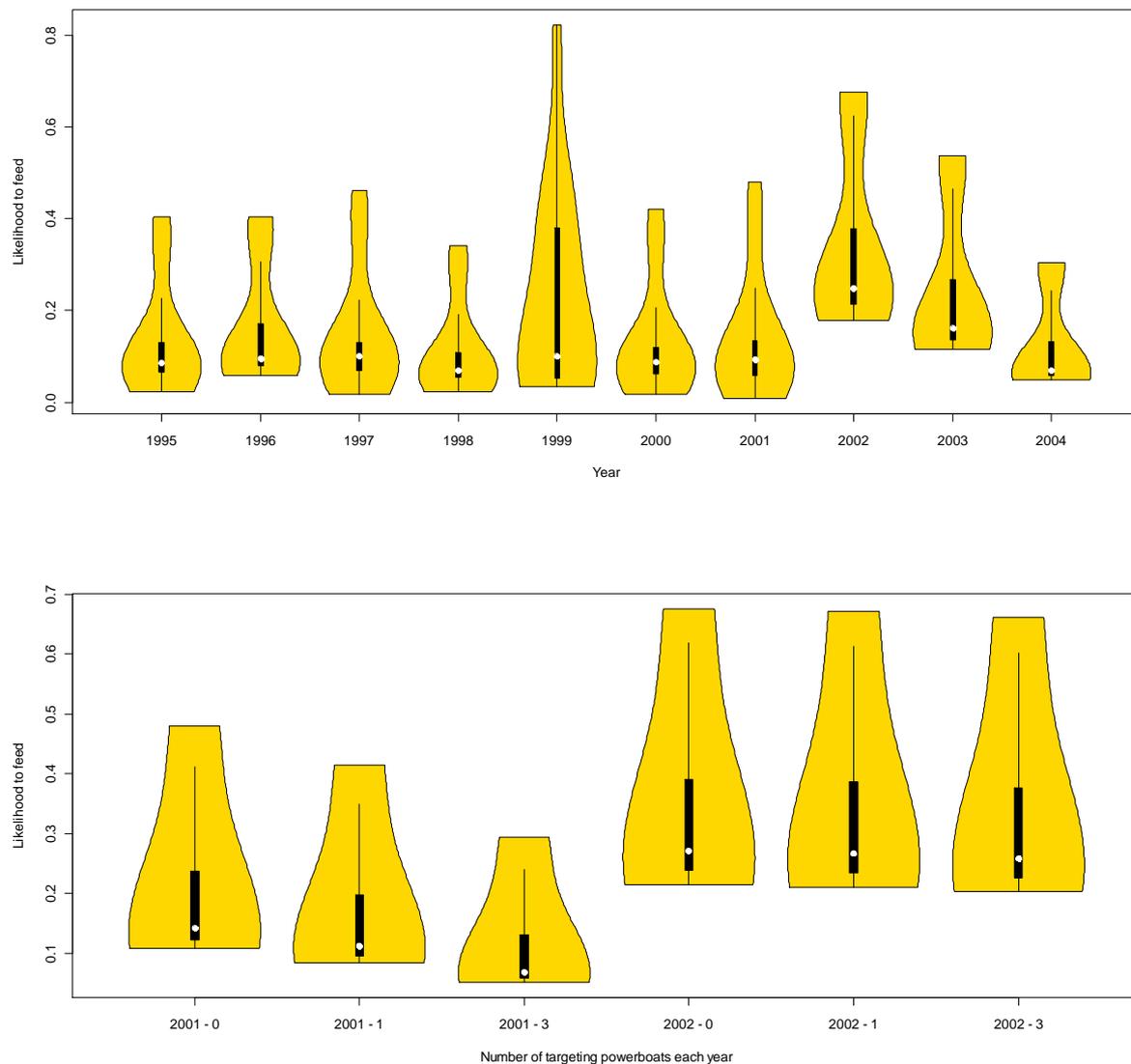


Figure 4. (a) inter-annual variation in the predicted probability that killer whales schools fed in the study area and (b) illustration of the varying effect of targeting powerboat presence on the predicted probability to observe killer whales foraging depending on years. Violin plots (boxplot and kernel density plot combined) of predicted likelihood to forage (GEE_{FT}) in 2001 and 2002 without targeting powerboats and with one or three of them for a median size school of whales and all months.

Discussion

Management implications

This study shows that silent vessels (kayaks) can elicit similar avoidance tactics than others that have an acoustic signature. This finding echoes previous studies that also showed that boat behavior and not boat type was the dominant factor influencing the elicitation of avoidance responses to boat interactions in bottlenose dolphins (Lusseau 2006, Lusseau 2003a). This finding also has important consequences for the debate surrounding acoustic disturbances (NRC 2005). While zones of injuries can be clearly defined *a priori*, with some limitations, the zones of influence of an acoustic cue are more difficult to ascertain, and regulatory bodies are now using an intensity threshold to determine how far those spread. This study shows that the zone of influence of a disturbance is not related solely to its acoustic intensity (how loud it sounds underwater), but whether it can be detected at all, and therefore it is highly likely that zones of influence of acoustic disturbances are much greater than we currently estimate.

Here we show that resident killer whales appear to adopt different tactics to cope with different vessel types. Killer whales also have different tactics to deal with variation in vessel number (Williams and Ashe 2007). Regardless of vessel type, activity disruption will have consequences for energetic demand and intake of these whales. Consistent with previous studies (Williams et al. 2006; Lusseau et al. 2009) our results show that the odds of killer whales feeding was decreased in the presence of ‘targeting’ powerboats. This means that vessels more likely to engage in interactions with whales are more prone to disrupt their behavior. Taken together, these findings show that killer whales have evasive tactics that are tuned to minimize perceived risks posed by vessels behaving like predators (stalking them). The inter-annual variability in the probability to observe whales feeding and the associated yearly variation in boat presence effect show that killer whales then adjust their response to those risks to try to maximize prey consumption given the costs of the risk.

Given the potential population-level implications associated with increase in energetic demand (Williams et al. 2006, Williams and Noren 2009) and decreased time feeding (Williams et al. 2006, Lusseau et al. 2009), we see a strong need for a “No-go” MPA that applies to all vessel types (Ashe et al. 2010). A “No-go” MPA would provide a research area in which temporary exemptions could be made for kayaks to enter while researchers are conducting dedicated kayak-only experiments. These fine-scale behavioral studies could be conducted to assess behavioral responses to kayak number, distance and activity, in order to refine, kayak-specific guidelines in future. A high-level of compliance with the boundaries of the MPA would be required to successfully execute controlled vessel experiments (Williams et al. 2002a, 2002b, Williams and Ashe 2007). Alternatively, such experiments could be carried-out with the NRKW population. The behavioral responses to kayaks observed here warrant further attention to test/inform existing kayaking guidelines around both northern and southern residents outside ‘No-go’ zones and MPAs.

Acknowledgements

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References

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- Ashe, E., Noren, D.P. and Williams, R. 2010. Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Animal Conservation* 13:196-203.
- Bain, D.E. and Dahlheim, M.E. 1994. Effects of masking noise on detection thresholds of killer whales. In (T. R. Loughlin, ed.) *Marine Mammals and The Exxon Valdez*. Academic Press. N.Y. 243-256.
- Barrett-Lennard, L.G., Ford, J.K.B., Heise, K.A. 1996. The mixed-blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* 51: 553-565.
- Burnham, K. P. and Anderson, D. R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd ed. Springer.
- Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Marine Mammal Science* 18:394–418.
- Felleman F.L., Heimlich-Boran, J.R., Osborne, R.W. 1991. Feeding ecology of the killer whale (*Orcinus orca*). In: Pryor K, Norris KS (eds) *Dolphin societies*. University of California Press, Berkeley, CA, p 113–147.
- Foote, A.D., Osborne, R.W., Hoelzel, A.R. 2004. Whale-call response to masking boat noise. *Nature* 428:910.
- Ford, J.K.B, Ellis G.M., Balcomb, K.C. 2000. *Killer whales: the natural history and genealogy of Orcinus orca in British Columbia and Washington State*, 2nd edn. University of British Columbia Press, Vancouver, BC.
- Ford, J.K.B., Ellis, G.M. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series* 316:185–199.

- Ford, J.K.B., Ellis, G.M., Olesiuk, P.F., Balcomb, K.C. 2010. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology Letters*. 6:139-142.
- Gregory, P.R. and Rowden, A. 2001 Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals* 27.2: 105-113.
- Henry, E. and Hammill, M.O. 2001. Impact of small boats on the haulout activity harbor seals (*Phoca vitulina*) in Métis Bay, Saint Lawrence Estuary, Québec, Canada. *Aquatic Mammals* 27.2: 140-148.
- Hoelzel, A.R. 1993. Foraging behaviour and social group dynamics in Puget Sound killer whales. *Animal Behaviour* 45: 581–591.
- Holt, M.M., Noren, D.P., Veirs V., Emmons C., Veirs, S. 2003. Speaking up: killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *Journal of the Acoustical Society of America*, 125:EL27–EL32.
- Kriete, B. 1995. Bioenergetics in the killer whale, *Orcinus orca*. Unpublished PhD thesis, University of British Columbia, Vancouver, B.C. 138 pp.
- Lusseau, D. 2003a. Male and female bottlenose dolphins have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series*, **257**, 267–274.
- Lusseau, D. 2003b. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology*, **17**, 1785-1793.
- Lusseau, D. 2006. The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Marine Mammal Science*, **22**, 802–818.
- Lusseau, D., Williams, R. J., Wilson, B., Grellier, K., Barton, T. R., Hammond, P. S. & Thompson, P. M. 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters*, **7**, 1068-1076.
- Morton, A. B. and H. K. Symonds. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES Journal of Marine Science*. Volume 59, 71 to 80.
- Noren, D.P., Johnson, A.H., Rehder, D., Larson, A. 2009. Close approached by vessels elicit surface active behaviors by southern resident killer whales. *Endangered Species Research*. 8: 179-192.
- NRC (National Research Council). 2005. Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. Washington, DC: National Academy Press.
- R Development Core Team 2005. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, <http://www.R-project.org/>.
- Ward, E. J., Holmes, E. E. and Balcomb, K. C. 2009. Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology*. 3: 632-640.

- Williams, R., Trites, A.W., Bain, D.E. 2002a. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, London. 256:255–270.
- Williams R., Bain D.E., Ford J.K.B., Trites, A.W. 2002b. Behavioural responses of male killer whales to a 'leapfrogging' vessel. *Journal of Cetacean Research and Management*. 4:305–310.
- Williams, R., Lusseau, and Hammond, P.S. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation* 133(3): 301-311.
- Williams, R. and Ashe, E. 2007. Killer whale evasive tactics vary with boat number. *Journal of Zoology* (London) 272(4): 390-397.
- Williams R., Bain D.E., Smith, J.C., Lusseau, D. 2009a. Effects of vessels on behaviour patterns of individual southern resident killer whales *Orcinus orca*. *Endangered Species Research* 6: 199–209.
- Williams, R., Lusseau, D. and Hammond, P.S. 2009b. The role of social aggregations and protected areas in killer whale conservation: the mixed blessing of critical habitat. *Biological Conservation* 142:709-719.
- Williams, R. and Noren, D.P. 2009. Swimming speed, respiration rate and estimated cost of transport in killer whales. *Marine Mammal Science* 25:327-350.
- Yan J (2002). "geepack: Yet Another Package for Generalized Estimating Equations." *R News*, **2**, 12–14.

ELECTRONIC SUPPLEMENTARY INFORMATION

Table 1. Model selection and likelihood ratio tests assess the significance of the boat effect. AIC are corrected for sample size.

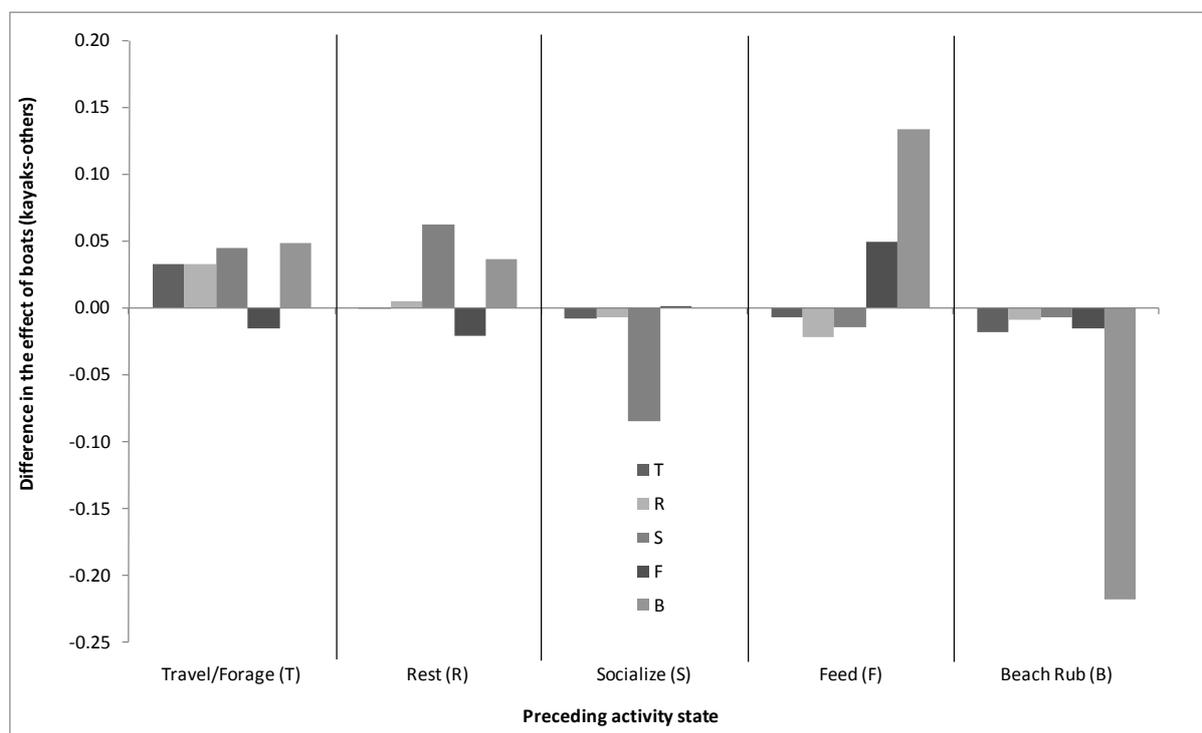
Model	Component added	Significance	AIC
PS, BP	BS,BPS	Δ deviance=92, Δ df=20, $p < 0.0001$	418
BPS			366

Table 2. Model selection and likelihood ratio tests assess the significance of the boat presence (B) and boat type effects (T) and contrast these two effects. AIC are corrected for sample size. In these models boat type refers to three boat categories.

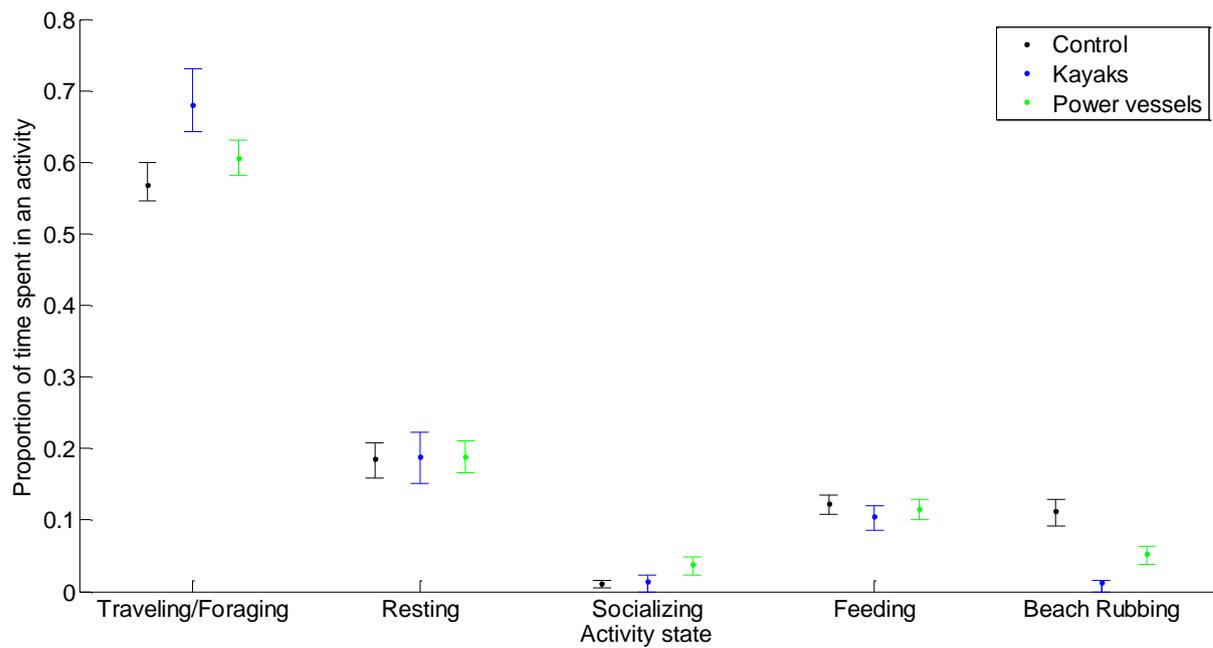
Model	Component added	Significance	AIC
PS, BTP	BS,BPS	Δ deviance=167.2, Δ df=20, $p < 0.0001$	698
BPS, BTP			646
PS,BTP	TS,TPS	Δ deviance=167.2, Δ df=60, $p < 0.0001$	698
TPS, BTP			651

Table 3. Model selection and likelihood ratio tests assess the significance of the boat presence (B) and boat type effects (T) and contrast these two effects. AIC are corrected for sample size. In these models boat type refers to two boat categories.

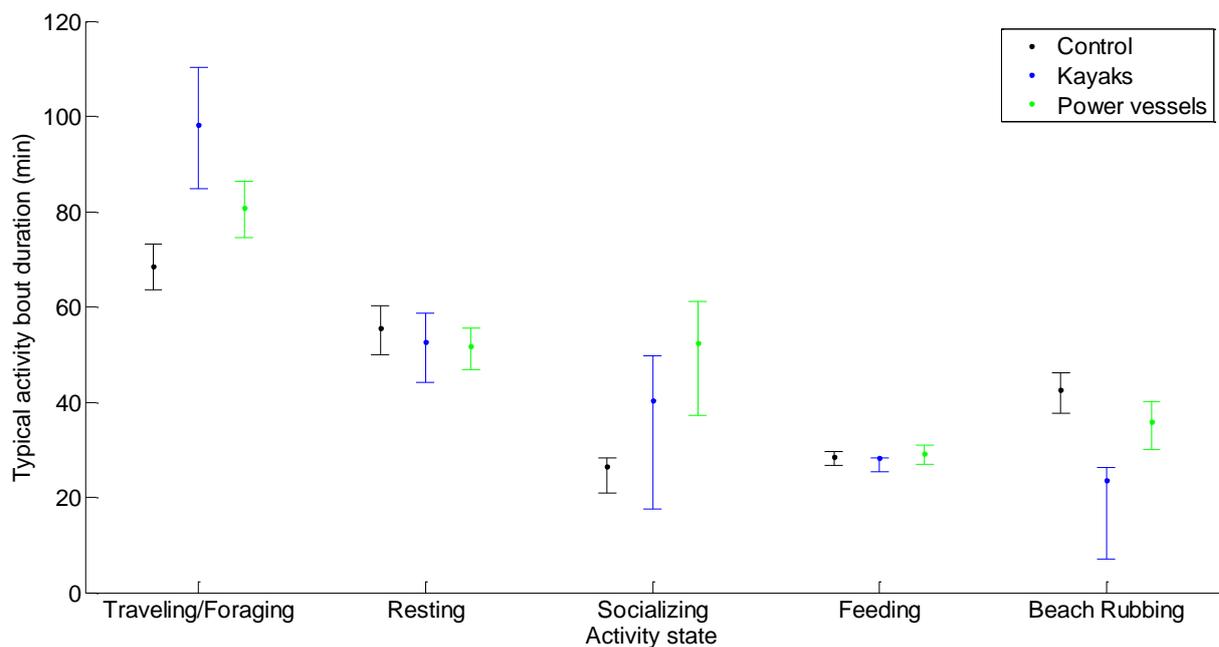
Model	Component added	significance	AIC
PS, BTP	BS,BPS	Δ deviance=167.2, Δ df=20, $p < 0.0001$	555.6
BPS, BTP			503.3
PS,BTP	TS,TPS	Δ deviance=167.2, Δ df=60, $p < 0.0001$	555.6
TPS, BTP			504.9



SI Figure 1. Difference between the transition probability of the kayak chains and the other boat chains. A positive value on the y-axis means that the transition probability of the kayak chain was higher than the 'other vessels' one.



SI Figure 2. The activity budget of killer whales off the Robson Bight reserve when exposed to the three boat treatments (control, kayak, other vessels). Error bars are 95% bootstrapped confidence intervals.



SI Figure 3. Typical activity bout duration (in min.) off the Robson Bight reserve when exposed to the three boat treatments (control, kayak, other vessels). Error bars are 95% bootstrapped confidence intervals.

GEE Model selection

Table 4. Fit of contrasting GEE models to explain the likelihood to observe killer whales foraging including goodness-of-fit Pearson's χ^2 statistics and QIC for model selection. All models have a first-order autoregressive correlation structure.

Independent variables equation	χ^2 , df, p-value	QIC	Δ QIC
Year,Month,School size	130, 1725, ns	11102	42
Year,Month,School size,all powerboat presence	141.9, 17249, ns	11088	28
Year,Month,School size,all power boat	132.4, 17249, ns	11103	43
Year,Month,School size,all powerboat presence,kayak presence	134.2, 17248, ns	11077	17
Year,Month,School size,kayak presence	129.5, 17249, ns	11096	36
Year,Month,School size, kayaks	131.4, 17249, ns	11100	40
Year,Month,School size,all power boats,kayak presence	130.9, 17248, ns	11098	38
Yearxall power boats,Month,School size	130.7, 17240, ns	11087	27
Yearxkayak presence,Month,School size	127.5, 17240, ns	11108	48
Monthxall power boats,Year,School size	131.2, 17246, ns	11097	37
Monthxkayak presence,Year,School size	133.6, 17246, ns	11092	32
Yearxall powerboat presence,Month,School size	133.9, 17240, ns	11073	13
Year,Month,School size,targeting power boat presence	132.4, 17249, ns	11060	0
Year,Month,School size,targeting power boats	141.9, 17249, ns	11088	28
Year,Month,School size,targeting power boat presence,kayak presence	132.3, 17248, ns	11061	1
Year,Month,School size,targeting power boats,kayak presence	140.3, 17248, ns	11087	27
Yearxtargeting power boats,Month,School size	133.5, 17240, ns	11064	4
Monthxtargeting power boats,Year,School size	145.7, 17246, ns	11090	30
Yearxtargeting power boat presence,Month,School size	130.8, 17240, ns	11065	5

Table 5. Fit of contrasting GEE models to explain the likelihood to observe killer whales foraging including goodness-of-fit Pearson's χ^2 statistics and QIC for model selection. All models have a first-order autoregressive correlation structure.

Independent variables equation	χ^2 , df, p-value	QIC	Δ QIC
Year,Month,School size	1288, 17250, ns	21106	1
Year,Month,School size,all powerboat presence	1291,17249, ns	21116	11
Year,Month,School size,all power boat	1288, 17249, ns	21108	3
Year,Month,School size,all powerboat presence,kayak presence	1290, 17248, ns	21113	8
Year,Month,School size,kayak presence	1289, 17249, ns	21105	0
Year,Month,School size, kayaks	1289, 17249, ns	21110	5
Year,Month,School size,all power boats,kayak presence	1289, 17248, ns	21109	4
Yearxall power boats,Month,School size	1284, 17240, ns	21139	34
Yearxkayak presence,Month,School size	1287, 17240, ns	21131	26
Monthxall power boats,Year,School size	1289, 17246, ns	21121	16
Monthxkayak presence,Year,School size	1290, 17246, ns	21116	11
Yearxall powerboat presence,Month,School size	1290, 17240, ns	21144	39
Year,Month,School size,targeting power boat presence	1291, 17249, ns	21117	12
Year,Month,School size,targeting power boats	1291, 17249, ns	21116	11
Year,Month,School size,targeting power boat presence,kayak presence	1291, 17248, ns	21114	9
Year,Month,School size,targeting power boats,kayak presence	1291, 17248, ns	21116	11
Yearxtargeting power boats,Month,School size	1296, 17240, ns	21150	45
Monthxtargeting power boats,Year,School size	1292, 17246, ns	21127	22
Yearxtargeting power boat presence,Month,School size	1295, 17240, ns	21146	41

Table 6. Fit of contrasting GEE models to explain the likelihood to observe killer whales foraging instead of traveling including goodness-of-fit Pearson's χ^2 statistics and QIC for model selection. All models have a first-order autoregressive correlation structure.

Independent variables equation	χ^2 , df, p-value	QIC	Δ QIC
Year,Month,School size	198.7, 17250, ns	10402	33
Year,Month,School size,all powerboat presence	208.3, 17249, ns	10390	21
Year,Month,School size,all power boat	200.4, 17249, ns	10402	33
Year,Month,School size,all powerboat presence,kayak presence	199.4, 17248, ns	10380	11
Year,Month,School size,kayak presence	198.2, 17249, ns	10395	26
Year,Month,School size, kayaks	200.7, 17249, ns	10400	31
Year,Month,School size,all power boats,kayak presence	199.2, 17248, ns	10396	27
Yearxall power boats,Month,School size	197.1, 17240, ns	10388	19
Yearxkayak presence,Month,School size	196.9, 17240, ns	10406	37
Monthxall power boats,Year,School size	199.7, 17246, ns	10399	30
Monthxkayak presence,Year,School size	202.6, 17246, ns	10391	22
Yearxall powerboat presence,Month,School size	197.5, 17240, ns	10377	8
Year,Month,School size,targeting power boat presence	199.8, 17249, ns	10369	0
Year,Month,School size,targeting power boats	208.3, 17249, ns	10390	21
Year,Month,School size,targeting power boat presence,kayak presence	199.7, 17248, ns	10369	0
Year,Month,School size,targeting power boats,kayak presence	206.7, 17248, ns	10388	19
Yearxtargeting power boats,Month,School size	201, 17240, ns	10370	1
Monthxtargeting power boats,Year,School size	212.5, 17246, ns	10394	25
Yearxtargeting power boat presence,Month,School size	198.1, 17240, ns	10375	6

GEE – selected model for each activity state

Table 7. Table of coefficients for the model selected to explain the likelihood that whales were observed foraging in contrast with performing any other activity. Information on the variance and covariance components are provided in Table 2 (p-value: <0.001 ‘***’; 0.001 ‘**’; 0.01; ‘*’ 0.05).

Component	coefficient	SE	Wald’s χ^2
Intercept	0.00049	0.308	0.00
Year – 1996	-0.015	0.128	0.01
1997	0.123	0.127	0.9
1998	-0.290	0.127	5.3*
1999	-0.809	0.222	13.3***
2000	0.0007	0.120	0.00
2001	0.190	0.126	2.3
2002	1.184	0.127	86.4***
2003	0.581	0.130	20.0***
2004	-0.301	0.142	4.5*
Month – July	-1.398	0.295	22.5***
August	-1.824	0.295	38.2***
September	-1.577	0.311	25.7***
School size	-0.122	0.0098	153.3***
Targeting powerboat – present	-0.353	0.0606	34.0***

Table 8. Table of coefficients for the model selected to explain the likelihood that whales were observed traveling in contrast with performing any other activity. Information on the variance and covariance components are provided in Table 3 (p-value: <0.001 ‘***’; 0.001 ‘**’; 0.01; ‘*’ 0.05).

Component	coefficient	SE	Wald’s χ^2
Intercept	-0.118	0.258	0.2
Year – 1996	-0.360	0.096	14.0***
1997	-0.343	0.098	12.3***
1998	-0.071	0.090	0.6
1999	-0.366	0.135	7.3**
2000	-0.168	0.090	3.5
2001	-0.177	0.097	3.4
2002	-0.451	0.103	19.1***
2003	-0.233	0.100	5.4*
2004	0.116	0.102	1.3
Month – July	1.328	0.249	28.3***
August	1.445	0.250	33.4***
September	1.670	0.261	40.8***
School size	-0.019	0.004	24.4***
Kayak – present	0.124	0.0626	3.9*

Table 9. Table of coefficients for the model selected to explain the likelihood that whales were observed foraging in contrast with traveling. Information on the variance and covariance components are provided in Table 4 (p-value: <0.001 ‘***’; 0.001 ‘**’; 0.01; ‘*’ 0.05). The Year base level for this analysis was changed to 1999, the year when the likelihood to forage was the lowest.

Component	coefficient	SE	Wald’s χ^2
Intercept	-0.696	0.386	3.2
Year – 1995	0.942	0.264	12.8***
1996	0.940	0.260	13.0***
1997	1.172	0.261	20.1***
1998	0.665	0.260	6.6*
2000	1.009	0.259	15.2***
2001	1.247	0.261	22.8***
2002	2.061	0.260	63.0***
2003	1.477	0.262	31.8***
2004	0.502	0.269	3.5
Month – July	-1.602	0.303	28.0***
August	-2.031	.0305	44.5***
September	-1.851	0.322	33.0***
School size	-0.097	0.009	111.6***
Number of targeting powerboats	0.286	0.097	8.64**
Year – 1995 x targeting powerboats	-0.416	0.116	12.9***
1996 x targeting powerboats	-0.321	0.115	7.7**
1997 x targeting powerboats	-0.467	0.114	16.8***
1998 x targeting powerboats	-0.391	0.113	11.9***
2000 x targeting powerboats	-0.457	0.125	13.4***
2001 x targeting powerboats	-0.552	0.127	18.9***
2002 x targeting powerboats	-0.309	0.106	8.5**
2003 x targeting powerboats	-0.301	0.100	9.0**
2004 x targeting powerboats	-0.295	0.101	8.5**

**R code – Retrieving Pan’s Quasi-Akaike Information Criterion from geeglm objects
(geepack library)**

geepack does not have a function to estimate QIC for GEEs. We therefore derived one using the outputs from geeglm:

```
'QIC'<-function (model, dependent) {  
  
# this function calculates Pan's QIC for a binomial GEE implemented using geeglm from the  
geepack library  
  
fit<- model$fitted  
  
# vbeta robust parameter covariance matrix  
  
# vbeta.naiv naive parameter covariance matrix  
  
-2 * sum(dependent * log(fit/(1 - fit)) + log(1 - fit)) + 2  
*sum(diag((solve(model$geese$vbeta.naiv)) %*% model$geese$vbeta))  
  
}
```