

Meta-analyses of whalewatching impact studies: differences and similarities in disturbance responses among species.

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Abstract

Whalewatching activities are known to induce anti-predatory responses in the animals targeted by this industry. While the long-term consequences of these responses are still poorly understood, defining linkage between short-term effects and population level consequences is crucial to properly manage whalewatching industry. In this study we aim to assess the consistency of anti-predatory responses within and between species and to infer from them the physiological and long-term consequences of whalewatching disturbance. Using meta-analyses, we tested whether changes in speed, activity budget, inter-breath intervals, deviation and directness index were recorded during whalewatching interactions. We also assessed if these changes were due to covariates such as body size, species, presence of whalewatching regulations, habitat type and the quality of each study. Our findings confirm an effect of whalewatching activities across all studies. Directness of the path and changes in the activity budget were the most consistent variables across studies. The effect of boats on the odds of observing animals resting depended on body size, with smaller animals being less likely to rest in the presence of boats. Both of these proxies reflect greater direct energy expenditure and a loss in energy acquisition respectively. Future studies will aim to determine which abiotic (e.g. number of boats, proximity, etc.) or biotic (e.g. sex, group size, etc.) factors affect the most the behavioural changes to ultimately minimise the disturbance.

Introduction

Whalewatching has been conducted for over 60 years (Hoyt 2001) and it has grown into a worldwide and profitable industry (O'Connor et al. 2009) with a greater income than fisheries and aquaculture combined (Lusseau et al. submitted). Eco-tourism has the potential to enhance conservation measures in coastal communities providing an alternative to direct consumption of top predators (Karczmarsky, 2000). However, concerns on the effects of whale watching disturbance on the target animals aroused and several studies focused on whalewatching impact. Previous studies report a negative impact of this recreational activity on wildlife population (Carney and Sydeman 1999; Lusseau and Bejder 2007; Reed and Merenlender 2008). Several studies demonstrated behavioural disturbances among marine mammals in response to whalewatching activities. Short-term effects include changes in respiration patterns (Hastie et al. 2003; Tosi and Ferreira 2008; Senigaglia and Whitehead 2011), behavioural disruptions (Williams et al. 2002; Lusseau 2003a; Constantine et al. 2004; Stocking et al. 2008; Lusseau et al. 2009; Christiansen et al. 2010; Visser et al. 2011), modification of movement patterns involving vertical and horizontal avoidance (Frid and Dill 2002; Lusseau 2003b; Jahoda et al. 2003; Ribeiro et al. 2005; Lemon et al. 2006; Williams et al. 2009), changes in within-group individual distance (Nowacek et al. 2001) and shift in vocalization frequency or amplitude (Erbe 2002).

The heterogeneity of responses within and between species cannot be underestimated as what could be an appropriate proxy for disturbance in one case, can be inadequate in other cases. In fact animals response to predation risk according to their environmental and social landscape making their responses case specific (Laundré, 2010; Heithaus et al., 2009). Animals adopt the appropriate response depending on several factors. Among others, factors as quality of the occupied area, availability of alternative sites, and knowledge of the area are known to lower risk perception and density of predators (Stankowitch et al. 2005). Morphology can also influence anti-predatory responses. Fast swimmers mysticetes with elongated body, as species of the Balaenopteraeidae family, will favour flight response over physical fight (Ford et al. 2005). On the contrary robust and more social animals may respond physically with a fight approach towards the predators. For instance Sperm whales position themselves in a "rosette" formation during killer whales attacks (Pitman et al. 2001; Reeves et al. 2006) while humpback and gray whales respond to predatory attacks by rolling over and thrashing flukes and flippers (Ford et al. 2005). These different anti-predator strategies have been analysed by Ford and Reeves (2008) for baleen whales in response to killer whales attacks. However how these strategies apply to other risks such as interactions with whalewatching boats has not been explored yet. Life history strategies may also influence these responses and we expect that species with similar strategy should respond in the same way. Cetacean species are K-selected (Nerini et al., 1984), so we can expect them to have adapted conservative behavioural tactics allowing them to prioritize survival over fitness-enhancing activities (Ghalambor and Martin, 2001). Moreover mysticetes are capital breeders and foraging and breeding are segregated in time. Thus disturbances occurring in foraging grounds may also severely affect reproductive success decreasing the available energy that can be transferred to calves (Christiansen et al. 2012). This study aims to compare the variation in short-term behavioural changes in response to exposure to whalewatching risk across a range of cetacean species that have varied life history strategies. We assessed observed variability in response to whalewatching exposure in several metrics, such as speed, path sinuosity, interbreath-intervals and activity budgets, to ascertain the effect of whalewatching on cetaceans.

Previous studies conducted in sites subjected to long-term exposure, report long-term consequences of cetacean tourism (Buckingham et al. 1999; Corkeron 2004; Bejder et al. 2006a; Bejder et al. 2006b; Lusseau 2004; Williams et al. 2006). In fact animals respond to a perceived predation risk, in this case whalewatching, by either fleeing or increasing their vigilance. Any response has an associated cost and in the first case the consequence of the disturbance stimulus is direct energy expenditure. While in case of an increase in vigilance the result may be a diminished energy intake because of missed feeding opportunities. The connection between short-term and long-term effects is still poorly understood. Hence research on the linkage between these two levels of impact should be encouraged. The LaWE project has been developed with the aim of understanding effects of whalewatching disturbance on demographic parameters of cetacean populations (SC/62/WW6). However determining effects on demographic parameters implies having a conspicuous data set over several generational periods and ideally data prior the beginning of the disturbance. The long life span of cetaceans, the cost associated with long-term monitoring and the practical difficulties of conducting impact studies (Corkeron, 2004) suggest the necessity of comparing long-term studies to contrast responses and trends of population consequence and their correlation with life history and ecological parameters. We meta-analysed results from a range of studies encompassing several species and sites to assess variability in behavioural effects. This approach allowed us to have replicates within species in different ecological conditions and between species.

Method

Study selection procedure

Mason et al. (2010) previously utilized meta-analysis for a preliminary study on cetaceans' response to whalewatching disturbance. In that case data have been collected only from published articles, however from the 55 reviewed articles only 5 have been judged suitable to be used in the analysis (Mason et al. 2009). The heterogeneity in study design and inconsistent reporting of results drastically reduced the sample size and consequently the power of the meta-analysis itself. Also a bias towards significant results is often reported when published studies are used for meta-analysis, a phenomenon known as the file drawer effect (Scargle, 2000). For these reasons we decided to take a different approach, contacting researchers directly.

We firstly sent a call for participation via the listserv of the cetacean specialist research community (MARMAM¹) and we received responses from 35 research groups (Lusseau and Senigaglia, 2011). Each research group was then asked to provide quality assurance and quality control procedures in place for data collection and archiving QA protocols were evaluated and scored as described in (see Appendix 1). Of the 21 researchers who sent their protocols, 16 research groups were further contacted to ask for summaries statistic data (see Appendix 1). We received data from 10 of the contacted research groups.

We defined disturbance as presence of whalewatching boats regardless of their numbers as this information was not available for every study. Because a disturbance response may vary

¹ MARMAM is a public mailing list dedicated to marine mammals research and management. At 2010 it counted more than 8,500 subscribers.

among species or across stimuli, we considered important to examine a variety of responses as wide as possible. Response variables encompassed changes in activity budget, respiration rates and several movement metrics including: deviation and directness index and speed (as defined Williams et al. 2002). Activity budget were defined by estimating activity transition matrices from focal follow group sampling behavioural sequences (Lusseau 2003a). Respiration rate was calculated as mean inter-breath intervals of the entire dive cycle hence including both dive and surface time; this value was then averaged across focal follows and among individuals.

Mean, median, mode, sample size, standard deviation and standard error of each response variable for each treatment level were provided. We defined disturbance as presence of whalewatching boats regardless of their numbers as this information was not available for every study. We obtained results from eight studies (all targeting odontocetes) for activity budget, seven studies (4 mysticetes and 3 odontocetes) for inter-breath interval and six studies (3 mysticetes and 3 odontocetes) for movement metrics, deviation and directness indices and speed (Table 1a,b).

Meta-analyses

We meta-analysed these results in order to assess the variability in effect size across species, taxa, and body size using package `metaphor` (Viechtbauer, 2010) in R (R version 2.11.0). the meta-analytical model is fitted as

$$y_i = \theta_i + e_i,$$

where i is the estimated effect size, y_i denotes the effect recorded in the i -th study, θ_i represents the true effect and e_i is the sampling error that is assumed to be normally distributed. However meta-analyses present an intrinsic heterogeneity by utilizing studies that are not identical in their methods or sample size. To account for this heterogeneity differences among studies may be modelled by adding moderators to the model. Thus the fitted model becomes a random effect model, where the true effect is specified as

$$\theta_i = \mu + u_i$$

where u_i is normally distributed and the aim becomes to estimate μ that is the average true effect and its heterogeneity (the variance associated with it). In this way we can examine how much the moderators influence the size of the mean true effect. In particular we explore quality of the study and targeted species as a source of heterogeneity. We also explored whether the presence of whalewatching regulations, official or voluntary, and the habitat type, breeding or feeding ground or resident, affect animals's responses to whalewatching disturbance. We grouped the studies by metrics used to evaluate whalewatching effects. However, we discarded a simple "vote-counting" approach of the statistically significant results to be able to weight each study according to their sample size. The null hypothesis in these meta-analyses was that the effect size was consistent across studies.

To examine changes in the activity budget we established an effect size by calculating the log odds ratio between impact and control situation for each study. This measure represents the probability of a particular activity to occur during control (absence of whalewatching boats) compared to impact situations (presence of whalewatching boats) accounting for differences in sample size. We utilized the log odds ratio values as the outcome measure (response

variable) and fitted the models using restricted maximum-likelihood that is considered unbiased and efficient (Viechtbauer, 2010). We also modelled the effect body size, estimated as known body length in the study areas. We used body size as a crude proxy for basal metabolic rate (Kleiber, 1947) and hence, as a proxy for physiological constraints. To examine whalewatching effects on inter-breath interval and movement metrics we calculated their standardized mean difference (SMD) as the outcome measures. SMD was calculated as the raw mean difference divided by the pooled standard deviation of the groups (Viechtbauer, 2010). The species and the quality of each study, the types of habitat represented by the study area and the presence of official or unofficial (voluntary) regulations have been used as moderators. We compared the different models using Akaike Information Criteria (AIC).

We could not assess differences in effect between sexes or in relation to disturbance intensity because such information was not available for every study.

Results

Consistency of behavioural response among species

On average there is no significant difference in speed between control and impact situations. However, dusky dolphins (species) in New Zealand seem to significantly decrease their speed when whalewatching boats are present while right whales in Argentina significantly increase their speed in impact situations (Figure 1). The path sinuosity, estimated as path deviation index, increased in impact situation although not significantly. Southern right whales in Argentina and minke whales in Iceland significantly increased their path deviation index in presence of whalewatching while humpback whales in New Caledonia show a smaller deviation index during treatment (Figure 2). Path linearity (path directness index) showed a significant difference between control and impact situations. Overall there is a decrease of path linearity when whalewatching boats were present (Figure 3). Humpback whales in Australia represent an exception by significantly increasing their path linearity during impact situation. In general animals show no significant changes in inter-breath intervals during impact situations. However both humpback whales in Australia and minke whales in Iceland have significantly shorter inter-breath intervals when whalewatching boats are present (Figure 4).

Activity budgets significantly differ as a consequence of whalewatching disturbance in most of the studies. Animals were more likely to be travelling, but not significantly, during impact situations (Figure 5) and less likely to be resting and foraging (Figure 6, 7). However, only the average effect of whalewatching boat presence on resting appeared to be significant.

Factors influencing differences in behavioural responses

None of the moderators that we tested had a significant influence on the observed variability in effect size among cetacean response to whalewatching; except for the effect of body size on the difference in proportion of time spent resting. Hence, neither accounting for the species, the quality of the study, presence of regulations nor the habitat type improved the fitness of the model (Table 2). However, accounting for body size, a proxy for basal metabolic rate, explained the difference in the observed effect on resting: the smaller the species (or

population, as populations of *Tursiops* varied greatly in body size) the smaller the odds that they would be resting in the presence of boats.

Discussion

We compared several impact studies to evaluate the effect of whalewatching across different cetacean species. Multiple response variables were examined to look for consistency in disturbance response. Characteristics of the study areas have been taken into account as possible explanation of the inter-study heterogeneity.

The pool of studies we used in our meta-analysis encompasses a wide variety of targeted species including mysticetes and odontocetes. We expected differences in the risk perception and response among species that differs in their behaviour, ecology and morphology. Fast species with elongated body evolved to reduced drag and improve swimming efficiency are likely to respond to predation risk by fleeing and hence increasing their speed (Ford et al. 2005; Christiansen et al. 2011). In the same way we might expect smaller cetacean that cannot rely on their ability to outpace a whalewatching motorboats, to adopt different anti-predatory techniques.

Our results support this hypothesis showing a slower speed of small dolphin as dusky dolphin during whalewatching encounter. Overall however, in contrast with previous study conducted by Mason et al (2010), speed does not seem to significantly change between impact and control situation. As previously suggested by Mason et al. mysticetes may suffer a smaller energetic cost due to increase high speed than odontocetes favouring fleeing as an escaping tactic. No significant changes in speed are detected for humpback whales in Australia or New Caledonia and this result seems consistent with what stated by Fort et al. (2005) on the differences in anti-predatory responses between fast and more bulky mysticetes. In fact body shape influences energetic costs. Species with elongated bodies as minke whales are efficient swimmers and may reach considerable speed, hence fleeing represents an efficient anti-predatory technique (Christiansen et al. 2011). However other more bulky species as humpback whales would favour “fight” over “flight” response and react to predators engaging in physical displays (Ford et al. 2005). Animals may also try to avoid boats by changing direction without leaving the area. If the patch is perceived of great importance and alternative areas are not available or are available only at great energetic expenses for the animals, abandoning the site even if just temporarily may result in a mal adaptive behaviour because of missed feeding opportunities. Hence animals may respond adopting an erratic path to avoid the boat without leaving the area. Our comparison among studies shows a tendency in increasing deviation index and a significant overall decrease in linearity, directness index, in presence of whalewatching boat. Moreover, specific escaping techniques may be efficient only under limited circumstances. Williams and Ashe (2007) report that killer whales responses vary with the number of boats. When few boats are present swimming speed of killer whales decrease and animals adopt an erratic path in order to avoid the boats without leaving the area. On the contrary when several boats are present, path linearity and speed both increases. At this stage we were not able to consider the number of boats present as we defined treatment as presence vs. absence of boats.

Previous studies report changes in dive and breathing pattern as a response to anthropogenic disturbance. Physiological responses to stress include increasing breathing rates while

increasing dive time can be an avoiding technique. Our definition of inter-breath interval encompasses both respiration rates and dive time so changes in inter-breath intervals reflects both vertical avoidance (longer dive time) and increased surface breathing. In accordance with finding from the previous meta-analyses conducted by Mason et al. (2010) our results do not show any changes in respiration pattern. Humpback whales in Australia and minke whales in Iceland represent an exception to the overall trend and show increasing inter-breath intervals during impact situation. This difference can be attributed to an easiness of collecting data of breathing and dive pattern on single whales compared to group of small dolphins. However humpback whales in New Caledonia show no differences in inter-breath intervals between impact and control situations.

Overall directness of the path and changes in the activity budget were the only variables consistently changing in response to whalewatching across studies and species. Changes in swimming pattern favouring a more direct path may be an escaping technique and can also be related with the higher amount of time spent travelling during whalewatching encounters. Although few studies have attempted to quantify energetic deficit caused by these tactics, the consequences of these responses are direct increase in energy expenditure and decreased opportunities to acquire energy. The magnitude of the disturbance response varied across studies. The likelihood that these behavioural disruptions will lead to impacts on the fitness of individuals will then depend on the ability those individuals will have to compensate for these effects.

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References

- Bejder L, Samuels A, Whitehead H, Gales N. 2006a Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Anim Behav* 72: 1149 – 1158
- Bejder L, Samuels A, Whitehead H, Gales N and others. 2006b Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv Biol* 20:1791 – 1798
- Buckingham C.A., Lefebvre L.W., Schaefer J.M., Kochman H.I. 1999. Manatee response to boating activity in a thermal refuge. *Wildlife Society Bulletin*, Vol 27, 2, pp 514-522
- Carney K.M. and Sydeman W.J. 1999. A Review of Human Disturbance Effects on Nesting Colonial Water birds. *The International Journal of Water bird Biology*, Vol. 22, No. 1, pp. 68-79
- Christiansen F., Lusseau D., Stensland E., Berggren P. 2010. Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endang Species Res*, Vol. 11: 91-99

- Christiansen, F., Rasmussen, M., Lusseau, D., 2011. Whalewatching boats disrupt the foraging activities of Minke whales in Faxaflói bay, Iceland. The Scientific Committee of the International Whaling Commission, Tromsø, Norway, Document SC/63/WW2.
- Christiansen, F., Rasmussen, M., Lusseau, D., 2012. Minke whales optimize swimming speed during interactions with whalewatching boats. Submitted to Biological Conservation
- Constantine R, Brunton D.H., Dennis T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biol Conserv* 117:299–307
- Corkeron P.J. 2004. Whale watching, iconography, and marine conservation. *Conserv Biol* 18:847–849
- 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.
- Ford J.K.B., Ellis G.M., Matkin D.R., Balcomb K.C., Briggs D., Morton A.B. 2005. Killer whale attacks on minke whales: prey capture and antipredator tactics. *Marine Mammal Science* 21: 603-618
- Ford J.K.B., Reeves R.R. 2008. Fight or flight: antipredator strategies of baleen whales. *Mammal Rev.* 38: 50-86
- Frid, A. & Dill, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11
- Jahoda M., Lafortuna C. L. Biassoni N. et al. 2003. Mediterranean fin whale's (*Balaenoptera physalus*) response to small vessels and biopsy sampling observed through passive tracking and timing of respiration. *Marine Mammals Science*, **19**, 96-110
- Hastie, G. D., B. Wilson, L. H. Tufft and P. M. Thompson. 2003. Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science* 19:74–84
- Heithaus, M. R., A. J. Wirsing, D. Burkholder, J. Thomson, and L. M. Dill. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78: 556-562
- Hoyt E (2001) Whale watching 2001: worldwide tourism numbers, expenditures and expanding socioeconomic benefits. International Fund for Animal Welfare, Yarmouth Port, MA
- Ghalambor C.K. Martin T. E. 2001. Fecundity-Survival Trade-Offs and Parental Risk-Taking in Birds. *Science* 292: 494-497
- Karczmarski L. 2000. Conservation and management of humpback dolphins: the South African perspective. *Oryx* 34: 207-211
- Kleiber M. 1947. Body size and metabolic rate. *Physiological Reviews* 27: 511-541
- Laundrè J.W., Hernandez L., Ripple W. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal*, **3**, 1-7

- Lemon Michelle, Lynch Tim P., Cato Douglas H., Harcourt Robert G. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. *Biological Conservation*, **127**, 363-372
- Lusseau D. 2003a. Effects of tour boats on the behaviour of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conserv Biol.* **17**, 1785–1793
- Lusseau D. 2003b. 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
- Lusseau D. 2004. The hidden cost of tourism: detecting long- term effects of tourism using behavioural information. *Ecol Soc* 9:2
- Lusseau D. and Bejder, L. 2007. The long-term consequences of short-term responses to disturbance: Experiences from whalewatching impact assessment. *International Journal of Comparative Psychology (Special Issue)* 20: 228-236.
- Lusseau D., Bain D.E., Williams R., Smith J.C. 2009. Vessel traffic disrupts the foraging behaviour of southern resident killer whales *Orcinus orca*. *Endang Species Res*, Vol. 6: 211–221
- Lusseau D. and Senigaglia V. 2011. Report on the first call for collaboration for LaWE. SC/63/WW4
- Lusseau D., Bejder L., Corkeron P., Allen S. and Higham J.E.S. submitted. Learning from past mistakes: Regulating whalewatching as a consumptive activity. *Conservation Letters*.
- Nerini, M.K., Braham, H.W., Marquette, W.M. and Rugh, D.J. 1984. Life history of the bowhead whale, *Balaena mysticetus*, (Mammalia, Cetacea). *J. Zool., London.* 204: 443-68.
- Nowacek, S. M., R. S. Wells, and A. R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* **17**:673–688.
- O' Connor S., Campbell R., Cortez H., Knowles T. 2009. Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits. *International Fund for Animal Welfare*, Yarmouth, MA.
- Pitman R., Baallance L., Mesnick S., Chiver S.J. 2001. Killer whale predation on sperm whales: observations and implication. *Marine Mammals Science*, 17(3): 494-507
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Reed S.E. and merenlender A.M. 2008. Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. *Conservation Letters* 1(3): 146-154.
- Reeves R.R., Berger J., Clapham P.J. 2006. Killer whales as predators of large baleen whales and sperm whales. Pag. 179-183 in J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams and R. L. Brownell, Jr., eds. *Whales, whaling and ocean ecosystems*. University of California Press, Berkeley, CA

- Ribeiro S., Viddi F.A., Freitas T.R.O. 2005. Behavioural Responses of Chilean Dolphins (*Cephalorhynchus eutropia*) to Boats in Yaldad Bay, Southern Chile. *Aquatic Mammals* 31(2), 234-242
- Scargle J. D. 2000. Publication bias: the “file-drawer” problem in scientific inference. *Journal of Scientific Exploration* 14:91-106
- Senigaglia V. and Whitehead H. 2011. Synchronous breathing by pilot whales. *Marine Mammals Science*. DOI: 10.1111/j.1748-7692.2011.00465.x
- Senigaglia V., de Stephanis R., Verborgh P., Lusseau D. 2012. The role of synchronized swimming as affiliative and anti-predatory behaviour in long-finned pilot whales. *Behavioural Processes* 0.1016/j.beproc.2012.04.011
- Stankowich T and Blumstein D.T. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. B* 272, 2627-2634
- Stockin K.A., Lusseau D., Binedell V., Wiseman N., Orams M.B. 2008. Tourism affects the behavioural budget of the common dolphin *Delphinus* sp. in the Hauraki Gulf, New Zealand. *Mar Ecol Prog Ser*, Vol. 355: 287–295
- Tosi C.H. and Ferreira R.G. 2008. Behaviour of estuarine dolphin, *Sotalia guianensis* (Cetacea, Delphinidae), in controlled boat traffic situation at southern coast of Rio Grande do Norte, Brazil. *Biodiversity and Conservation* Vol 18, 1: 67-78
- Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3), 1-48. URL <http://www.jstatsoft.org/v36/i03/>.
- Visser F., Hartman K.L., Rood E.J.J., Hendriks A.J.E. Zult D.B. et al. 2011. Risso’s dolphins alter daily resting pattern in response to whale watching at the Azores. *Marine mammals science* 27(2): 366–381
- Weinrich M., Lusseau D., Janiger D., Consoer M., Kirchner T., and Lundberg E. A Review and Meta-Analysis of Whalewatch Impact Studies. SC/60/WW10
- Williams, R. M., A. W. Trites, and D. E. Bain. 2002. 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, Lusseau D, Hammond P.S. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol Conserv* 133:301–311
- Williams R. and Ashe E. 2007. Killer whale evasive tactics vary with boat number. *Journal of Zoology* 272: 390–397
- Williams R., Bain D.E., Smith J.C., Lusseau D. 2009. Effects of vessels on behaviour patterns of individual southern resident killer whales *Orcinus orca*. *Endang Species Res.* Vol. 6: 199–209

Figures

Figure 1. Forest plot representing differences in speed between impact (presence of whalewatching boats) and control situations (absence of whalewatching boats) among studies. studies are listed by study area. The dotted line represents the “line of no effect”. The target species were Humpback whales in New Caledonia; Southern right whales in Peninsula Valdes, Argentina; Dusky dolphins in Goose bay, New Zealand; Killer whales off San Juan Island, USA; Humpback whales in Cape Moreton, Australia; Killer whales in Haro Strait, USA. The squares represent each study and their dimension is proportional to the sample size. The horizontal line crossing each squared represents the confidence intervals. The diamond represents the overall response so the differences occurring between treatment and control taking into account every study.

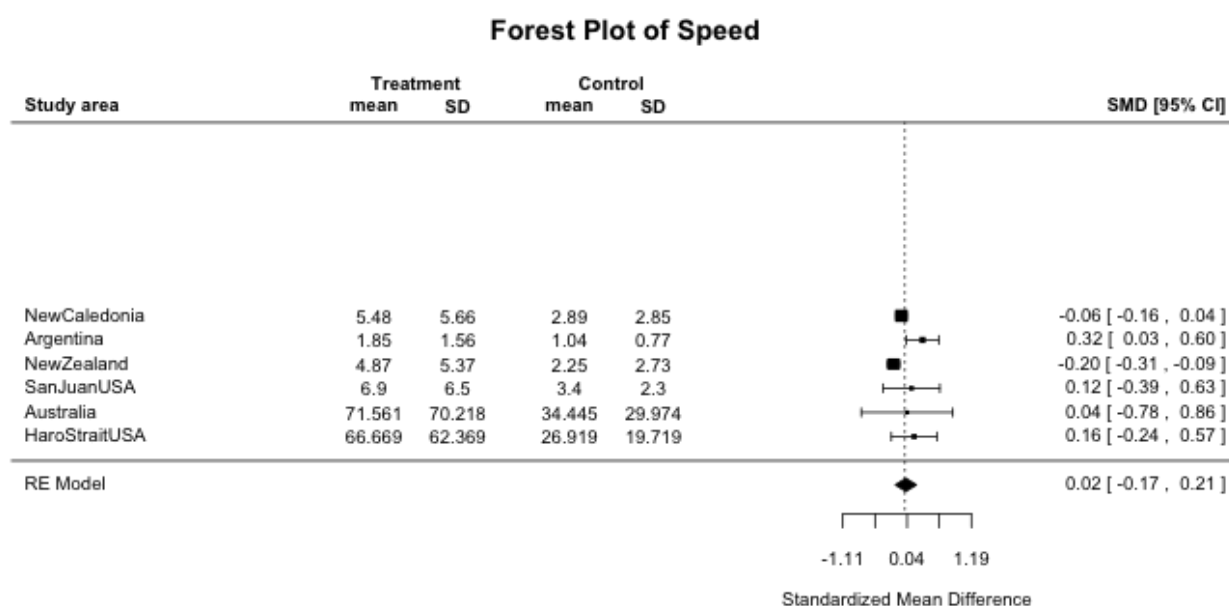


Figure 2. Forest plot representing differences in deviation index (measure of path sinuosity) between impact and control situations among studies. Studies are listed by study area. The dotted line represents the “line of no effect”. The target species were Minke whales in Faxaflói bay, Iceland; Humpback whales in New Caledonia; Southern right whales in Peninsula Valdes, Argentina; Dusky dolphins in Goose bay, New Zealand; Humpback whales in Cape Moreton, Australia; Killer whales in Haro Strait, USA. The squares represent each study and their dimension is proportional to the sample size. The horizontal line crossing each squared represents the confidence intervals. The diamond represents the overall response so the differences occurring between treatment and control taking into account every study.

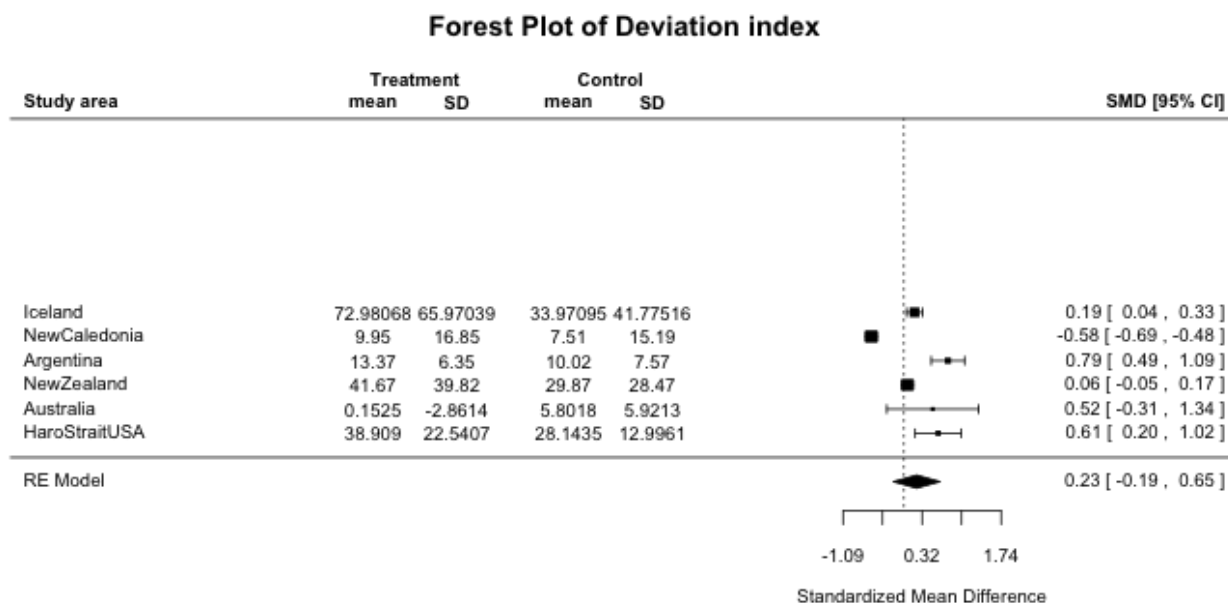


Figure 3. Forest plot representing differences in directness index (degree of path linearity) between impact and control situations among studies. Studies are listed by study area. The dotted line represents the “line of no effect”. The dotted line represents the “line of no effect”. The target species were Minke whales in Faxafloi bay, Iceland; Humpback whales in New Caledonia; Southern right whales in Peninsula Valdes, Argentina; Dusky dolphins in Goose bay, New Zealand; Humpback whales in Cape Moreton, Australia; Killer whales in Haro Strait, USA. The squares represent each study and their dimension is proportional to the sample size. The horizontal line crossing each squared represents the confidence intervals. The diamond represents the overall response so the differences occurring between treatment and control taking into account every study.

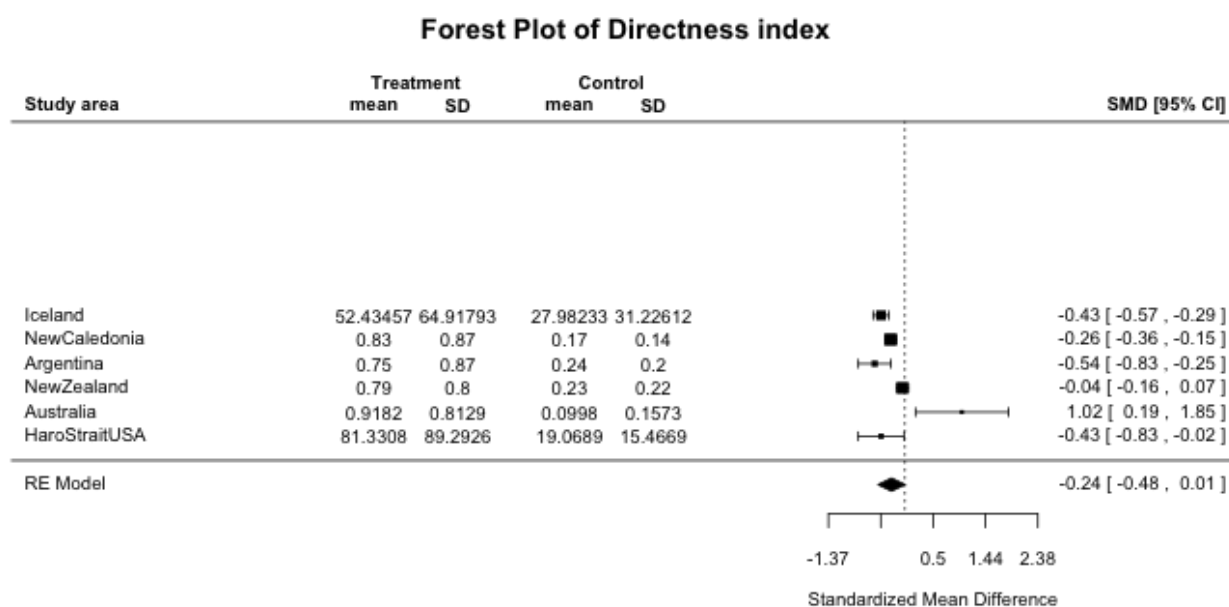


Figure 4. Forest plot representing differences in inter-breath interval between impact and control situations among studies. Studies are listed by study area. The dotted line represents the “line of no effect”. The dotted line represents the “line of no effect”. The target species were Minke whales in Faxaflói bay, Iceland; Bottlenose dolphins in Fjirdland, New Zealand; Humpback whales in New Caledonia; Killer whales off San Juan Island, USA; Humpback whales in Cape Moreton, Australia; Killer whales in Haro Strait, USA; Blue whales in the Gulf of California, Mexico. The squares represent each study and their dimension is proportional to the sample size. The horizontal line crossing each squared represents the confidence intervals. The diamond represents the overall response so the differences occurring between treatment and control taking into account every study.

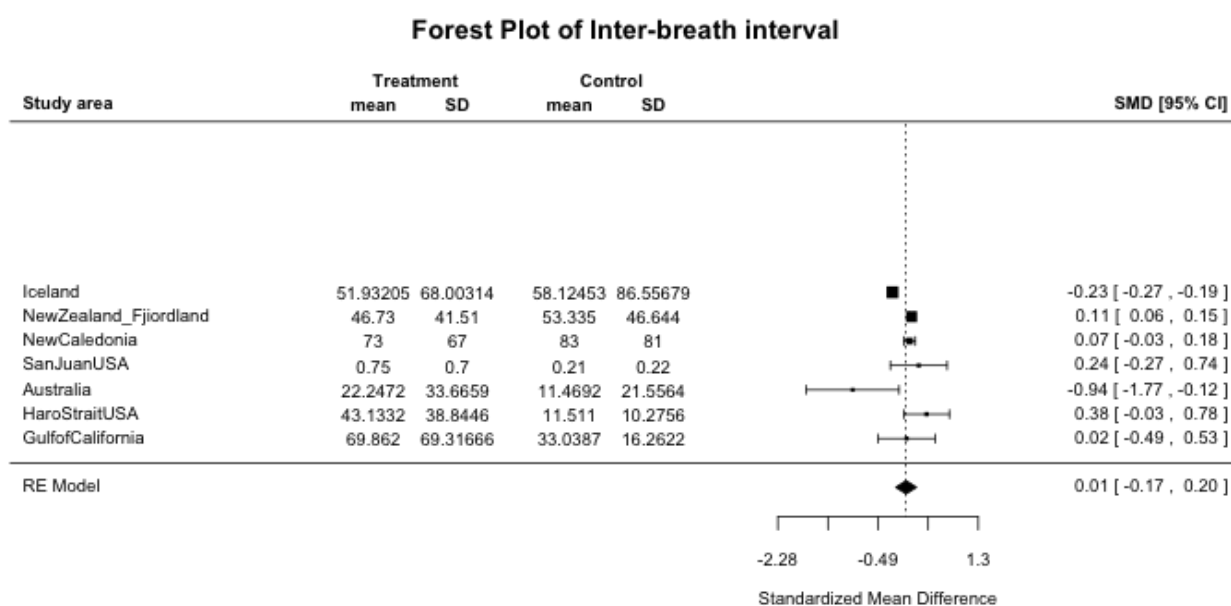


Figure 5. Forest plot showing differences in travelling behaviour among studies during impact and control situations. SRKW: southern resident killer whales off San Juan Island, USA. SB: bottlenose dolphins in Shark Bay, Australia. HAURAKI: common dolphins in the Hauraki Gulf, New Zealand. Zanzibar: bottlenose dolphins off Zanzibar Island, Tanzania. DS: bottlenose dolphins in Doubtful Sound, New Zealand. MS: bottlenose dolphins in Milford Sound, New Zealand. BANKS: Hector's dolphins off Banks Peninsula, New Zealand. NRKW: northern resident killer whales off Robson Bight reserve, Vancouver Island, Canada. Studies are ordered in an increasing order of time spent travelling in control situations. Values on the right are odds ratio with 95% confidence intervals for each study. Test for heterogeneity of residuals: $Q_7=81.2$ $p<0.0001$. The diamond (RE model) represents the estimated average log odds ratio with associated 95% confidence interval [-0.07;0.92].

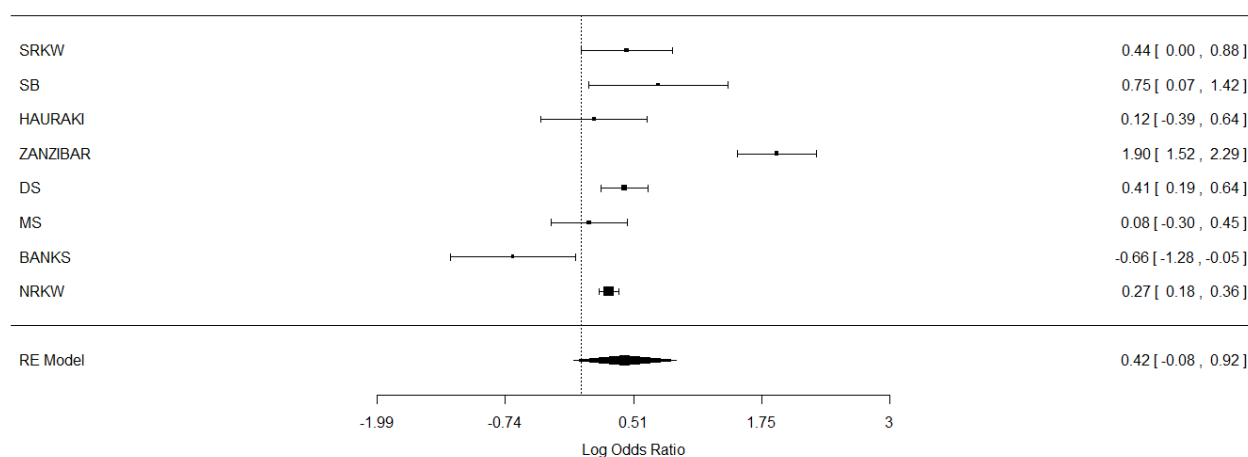


Figure 6. Forest plot showing differences in resting behaviour among studies during impact and control situations. SRKW: southern resident killer whales off San Juan Island, USA. SB: bottlenose dolphins in Shark Bay, Australia. HAURAKI: common dolphins in the Hauraki Gulf, New Zealand. Zanzibar: bottlenose dolphins off Zanzibar Island, Tanzania. DS: bottlenose dolphins in Doubtful Sound, New Zealand. MS: bottlenose dolphins in Milford Sound, New Zealand. BANKS: Hector's dolphins off Banks Peninsula, New Zealand. NRKW: northern resident killer whales off Robson Bight reserve, Vancouver Island, Canada. Studies are ordered in increasing length. Values on the right are odds ratio with 95% confidence intervals for each study. Test for heterogeneity of residuals: $Q_5=23.2$, $p=0.0003$. Test of moderator: $Q_1=4.1$, $p=0.04$. Estimated average log odds ratio: -1.9, 95% confidence interval [-3.26;-0.59]. Estimated average effect of length (body size) on log odds ratio: 0.33, 95% confidence interval [0.011;0.64]. AIC model with body size effect: 22.8, AIC of model presented: 22.2. Grey diamonds represent the fitted value, along with 95% confidence intervals, for each study.

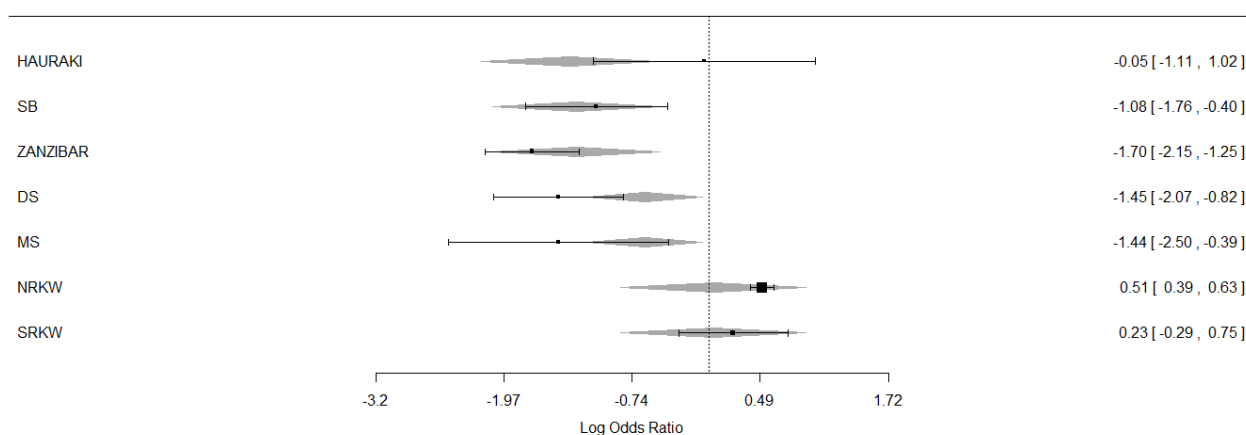
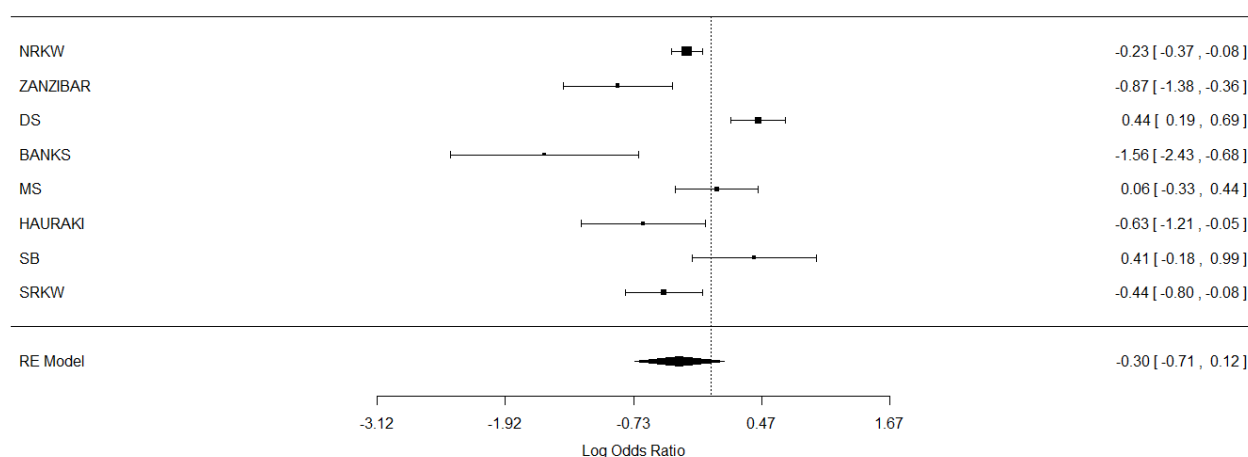


Figure 7. Forest plot showing differences in foraging behaviour among studies during impact and control situations. SRKW: southern resident killer whales off San Juan Island, USA. SB: bottlenose dolphins in Shark Bay, Australia. HAURAKI: common dolphins in the Hauraki Gulf, New Zealand. Zanzibar: bottlenose dolphins off Zanzibar Island, Tanzania. DS: bottlenose dolphins in Doubtful Sound, New Zealand. MS: bottlenose dolphins in Milford Sound, New Zealand. BANKS: Hector's dolphins off Banks Peninsula, New Zealand. NRKW: northern resident killer whales off Robson Bight reserve, Vancouver Island, Canada. Studies are ordered in an increasing order of time spent foraging in control situations. Values on the right are odds ratio with 95% confidence intervals for each study. Test for heterogeneity of residuals: $Q_7=49.5$, $p<0.0001$. The diamond (RE model) represents the estimated average log odds ratio with associated 95% confidence interval [-0.71;0.12].



Tables

Table 1a. This table summarized the main characteristics of the studies utilized in the meta-analyses. The author's name, the targeted specie, the habitat type, the subjective score given to the quality of each study, the geographical location where the study has been conducted and the presence of whale-watching approach regulation has been highlighted. Mysticetes are highlighted in yellow. (V) in the regulation column indicates the presence of a Voluntary code of conduct at the time when the study was conducted. Winter ground, under the Habitat column is a particular feeding ground in which researchers observed mating behaviour confirmed by progesterone analyses and calving. Information regarding each study are referred to the period in which the study has been conducted.

Study	Species	Habitat	Quality **	Site	Regulation
Christiansen et al.	Minke whale	Feeding ground	Excellent	Iceland	No
Christiansen et al. 2	Indo-pacific bottle.	Resident	Excellent	Zanzibar	No
Lusseau D.	Bottlenose dolphin	Resident	Excellent	New Zealand	Yes
Schaffar A.	Humpback whale	Migratory corridor	Good	New Caledonia	(V)
Lundquist D.	Right whale	Breeding ground	Excellent	Argentina	Yes
Lundquist D. 2	Dusky dolphin	Resident	Excellent	New Zealand	(V)
Williams et al.	NRKW	Resident	Excellent	Canada	Yes
Gendron D.	Blue whale	Winter ground	Good	Mexico	Yes
Noren D.	SRKW	Resident	Very good	USA	(V)
Smith JC	SRKW	Resident	Good	USA	(V)
Smith JC	Humpback whale	Migratory corridor	Good	Australia	Yes

** Subjective

Table 1b. This table summarize the different variables available for each study. For some of the studies several variables were available while for others only one variable was measured. Mysticetes are highlighted in yellow.

Study	Deviation I	Directness I	Inter-breath interval	Speed	Activity budget
Christiansen et al.	Yes	Yes	Yes	Yes	No
Christiansen et al. 2	No	No	No	No	Yes
Lusseau D.	No	No	No	No	Yes
Schaffar A.	Yes	Yes	Yes	Yes	Yes
Lundquist D.	Yes	Yes	No	Yes	Yes
Lundquist D. 2	Yes	Yes	No	Yes	Yes
Williams et al.	No	No	No	No	Yes
Gendron D.	No	No	Yes	No	No
Noren D.	No	No	Yes	Yes	No
Smith JC	Yes	Yes	Yes	Yes	No
Smith JC	Yes	Yes	Yes	Yes	No

Table 2. This table shows the AIC values per each model and each response variables. DevI is deviation index, DirI is directness index and IBI is inter-breath interval. Quality refers to the quality of the study; regulations refers to the presence of voluntary or official regulation for whalewatching activities; habitat refers to the habitat characteristics in relation to the targeted species (e.g. resident, feeding ground, breeding ground)

Model	Speed	DevI	DirI	IBI
No moderator	5.33	13.30	12.23	9.70
Quality	10.65	14.82	14.17	14.45
Species	9.81	15.02	15.32	16.24
Regulations	6.00	15.77	15.34	13.01
Habitat	9.35	15.00	15.29	14.57

Appendix 1

Report on the second call for collaboration on the LaWE project.

The rate of reply to the first call for data submitted to the marine mammal science community by LaWE was very promising. More than 30 research groups expressed interest in participating in the first phase of the project. Here we report on the following steps and particularly on the second call for data. We describe how communication have been handled, the tools used for a more efficient sharing of information and the results of this process. Considerations on data availability and analyses are also provided.

Method

We got in touch with the 35 research groups who reply to the first call to provide further information on the scope of the LaWE project and to ask for QA protocols to filter suitable studies. Initially few guidelines were provided on the format of QA protocols to allow higher flexibility in responses. However, after protocols examination individual researchers were contacted to request additional information if needed. QA protocols were evaluated considering the study area, the research platform and the targeted species, the observers' training and numbers and the length of data collection. For each type of data collected (behaviour, respiration rates, movement pattern and habitat use), survey and sampling method, existence of accuracy control of the measurement device and restricted weather condition under which data collection took place were evaluated. Only studies that collected data under control (defined as absence of boats) and treatment (defined as presence of boats) situations were considered. Also in case of data collected from research vessel, only studies that evaluated impact of research boat on the animals have been accepted. Based on the information provided in the protocols, a subjective score was given ranging between bad, fair, good, very good and excellent as outlined in Weinrich et al. SC/60/WW10.

All the researchers who sent their protocols except the ones rated as bad have been further contacted to ask for summaries statistic data. The quality of the studies will be considered during meta-analysis weighting each study accordingly. The data requested included mean, median, mode, sample size, standard deviation and standard error of each response variable. Response variables differed according to the type of data collected, behaviour, movement pattern, respiration rates and habitat use. Activity budgets were inferred from focal follow sequences. Deviation and directness index and speed as calculated in Williams et al. (2002) were used as measurements of movement pattern. Respiration rate was calculated as mean inter-breath intervals of the entire dive cycle; this value was then averaged across focal follow and among individuals. No studies on habitat use were considered suitable due to lack of data. The authors of the papers used in the previous meta-analysis (Weinrich et al. SC/60/WW10) have been directly contacted to ask for further data not available in the published manuscripts.

A website accessible by invitation only, has been created to provide detailed information on the LaWE project (<https://sites.google.com/site/lawescience/>). The website has been created using googlesite, which allows a good flexibility in creating interactive webpage and allows differential privacy setting. The website contains a descriptive section with a detailed description of the LaWE project scope and objectives and a page with the steering group

contact information. It also includes a calendar of activities with the deadlines of each step of the project. Moreover we created a section where the LaWE proposal and further reports presented at the International Whaling Commission have been uploaded and available for consultation and download. The website also provide project's news and updates and has a discussion section to allow share of comments and ideas from all the collaborators. In addition, every researcher who sent us QA protocols has been invited to join a googlegroup. This tool allows communicating with all the collaborators of the LaWE project and the Steering group using a single email address.

Research protocols have also been developed to ensure proper data collection and quality control in studies on whalewatching impact. These protocols are meant to be used as guidelines in future studies on whalewatching disturbance so that results from these studies could be added to the LaWE project. The protocols have been developed based on reviews of different methodology found in the literature, published studies with detailed and precise description of methodology, personal experience and input from QA protocols sent by the collaborators. A first draft of the protocols has been uploaded on a dedicated section of the LaWE website to ensure their easy accessibility to all collaborators.

Results

We received 21 protocols, excluding the ones sent by members of the Steering group. The correspondent studies covered a wide portion of the world and a high variety of species. Targeted species included blue, fin, humpback, southern right, minke and sperm whales. And from the delphinids family killer whales, bottlenose, striped and hector's dolphins.

Out of the 21 protocols 5 were graded as "excellent", 3 as "very good", 6 as "good", 1 "fair" and 3 "bad". Researchers of 2 studies belonging to the latter category welcomed the suggestions provided and agreed to use the developed protocols for further data collection. The remaining 4 protocols were lacking necessary information to be graded. We were unable to obtain the necessary information so we discarded the protocols. Out of the 16 studies considered suitable for the LaWE project 10 sent summaries statistic data while we are still waiting to hear from the remaining 6. We are also waiting for reply from authors of those papers used in the previous meta-analysis.

Conclusions

This part of the project was very successful and researchers were eager to collaborate. We received a good number of protocols and the majority of them were considered of suitable quality for being used in the meta-analysis. The aim of a meta-analysis is to combine and compare the results from several related studies. The data that we obtained cover a wide variety of study areas and targeted species and can be assumed randomly sampled from a larger normally distributed population of studies. Therefore we will be able to compare whalewatching effects under different ecological and anthropogenic pressure conditions. However data from Asia and Africa where whalewatching activities are known to influence cetacean behaviour (Christiansen et al. 2010; IFAW 2009) are lacking. It would be extremely interesting to include these two continents due to their importance for cetacean ecology and migrations and the threaten conservation status of many species (Corkeron et al. 2011).

The wide variety of response variables that we received was also very encouraging. In fact it enables us to evaluate whalewatching impact in a more complete way and to link it to energetic consumption during anti-predatory responses. Also the majority of the studies evaluate impact of disturbance according to individual, social and environmental differences. For instance differences among sexes or disturbance pressures have been evaluated. In a further stage of the analyses, these data will enable us to detect subtle and non-linear reaction of animals to disturbance and will allow us to provide ad-hoc guidelines to limit whalewatching impact.