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Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance

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ABSTRACT: Whale-watching activities can induce behavioral changes that may negatively affect cetacean populations. However, these changes may vary depending on species, populations and environmental features. It is important to determine inter-specific variation in cetacean responses to stressors in order to identify the best metrics for evaluation of consequences of anthropogenic disturbance. We used meta-analyses to assess the consistency of cetacean responses to whale-watching vessels across a pool of suitable studies covering a variety of species and sites. We analyzed several metrics to capture cetacean heterogeneous responses and to explore their reliability across species. We found disruptions of activity budget and of path directionality as the most consistent responses towards whale-watching vessels. In a similar manner across species, animals were more likely to travel and less likely to rest and forage in the presence of vessels. Cetaceans also showed a tendency to increase path sinuosity (deviation index) and decrease path linearity (directness index) during boat interactions. We also explored the influence of socio-ecological factors on behavioral response but found no consistent results among studies. Further population-specific studies should address the potential long-term consequences of these behavioral responses to inform management of the whale-watching industry.

KEY WORDS: Animal behavior · Disturbance response · Ecotourism · Activity budget · Random effect models · Odontocetes · Mysticetes

INTRODUCTION

Human recreational activities can induce behavioral and physiological changes in animal populations (Dyck & Baydack 2004). Whale-watching has been ongoing for more than 60 yr (Hoyt 2001), and it has grown into a worldwide lucrative industry (O'Connor et al. 2009). However, there are growing concerns about the effects of whale-watching activities on the targeted animals (Higham et al. 2014).

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Several studies focused on cetacean behavioral disruptions in response to whale-watching activities and found significant short-term effects (Williams et al. 2002, Lusseau 2003, Visser et al. 2011, Lundquist et al. 2012, Christiansen et al. 2013a,b) Some studies also report that long-term consequences on individual reproductive success and population size can arise due to repeated behavioral disruptions (Constantine et al. 2004, Bejder et al. 2006a,b).

Behavioral changes in response to whale-watching presence may vary among species and locations. The Order Cetacea includes a heterogeneous group of species with different physiological and ecological characteristics (e.g. different diving abilities, swimming limitations, different trophic level and social organization). Observed responses to whale-watching vessels include changes in respiration patterns (Hastie et al. 2003, Tosi & Ferreira 2008), activity budgets modifications (Lusseau et al. 2009, Christiansen et al. 2010, Visser et al. 2011), vertical and horizontal avoidance (Lemon et al. 2006, Williams et al. 2002), changes in inter-individual distance (Nowacek et al. 2001, Bejder et al. 2006a) and shift in vocalization frequency or amplitude (Erbe 2002, Holt et al. 2009). This variation in responses makes it challenging to evaluate whale-watching effects using a common proxy for disturbance. Moreover, it is difficult to assess whether these effects are limited to the targeted species/location, or if more general patterns exist. Thus, managers often operate without sufficient scientific data to ensure proper management of whale-watching tourism in data deficient areas. One way to overcome these difficulties is a meta-analytical approach that compares several studies and response patterns among different species and/or areas.

Meta-analysis allows for quantitative comparison between similarly conducted studies (Weinrich et al. 2010). In a meta-analysis, the results from each study are expressed as outcome measures, or effects size, and are computed on a common scale to allow for comparison (Viechtbauer 2010). This technique has been extensively used in animal ecology (Stankowich & Blumstein 2005, Nespolo & Franco 2007, Majolo et al. 2008) and was successfully applied to explore disturbance response of ungulates and anthropogenic impacts on Antarctic wildlife (Stankowich 2008, Coetzee & Chown 2015, Samia et al. 2015).

In this meta-analysis, we compared studies focusing on changes in activity budget, inter-breath interval and multiple movement metrics (speed, deviation index and directness index). These metrics have been previously independently addressed as appropriate proxies to determine responses to whale-watching disturbance (Williams et al. 2002, Lusseau 2003, Lundquist et al. 2012). The ecological conditions (habitat type, knowledge of the area, presence or absence of refuges) combined with species life history (late reproduction, low calving rate) and benefits from social living (cooperative defense, social cohesion, inter-generational transfer of knowledge) are likely to affect both the type of response and the way that repeated behavioral disruptions might influence population dynamics (Childress & Lung 2003, Wade et al. 2012). Thus, in our analysis we included the influence of habitat type and of eventual regulatory codes of whale-watching activities as well as differences between odontocetes and mysticetes, coarsely assuming all odontocetes as social species and all mysticetes as solitary. Furthermore, the cumulative time they are subjected to whale-watching disturbance may also differ between the 2 suborders; for example, mysticetes are capital breeders and they breed and forage in different locations at different times. They might, therefore, spend less time in an area targeted by whale-watching boats than resident odontocetes species that forage and breed in that area.

Our meta-analysis aimed to address the following questions: (1) Does whale-watching cause similar responses in different cetacean species and in different locations? (2) Are some metrics more reliable than others to capture heterogeneous cetacean responses? (3) Which factors (life history characteristics relating to suborder mysticetes or odontocetes, or ecological conditions relating to habitat type and presence or absence of regulatory measures) will most influence the type of behavioral response utilized by cetaceans? Finally, although not tested directly in this study, we highlight the necessity of population-specific studies to better evaluate potential long-term consequences and impact of whale-watching.

METHODS

Study selection procedure

Generally, meta-analyses utilize published studies; however, variations in the study design and a bias towards publishing only significant results often reduce the number of suitable studies (Scargle 2000, Tsilidis et al. 2013). Moreover, a previous meta-analysis from Weinrich et al. (2010) reported several limiting factors of this traditional approach. These authors made a systematic review of published literature but they were able to compare very few studies per variables (max. of 5) due to a wide array of

response variables. They also found notable heterogeneity in how response variables were measured and/or reported, thus hampering the possibility of inter-study and inter-species comparisons. For these reasons, we decided to take a different approach and contacted researchers directly to obtain the necessary measures of mean and SD to use in the meta-analyses. This approach permitted a more in-depth quality control of each study and allowed us to include also those studies that used comparable study designs and statistical methods but reported different values. In some cases in which raw data where comparable but statistical methodology differed among studies, we asked the researcher to standardize and re-analyze data.

We first sent a call for participation via the listserv of the cetacean specialist research community (MARMAM[1]) and received responses from 35 research groups (Lusseau & Senigaglia 2011). Each research group was asked to provide quality assurance and quality control procedures in place for data collection and archiving to evaluate study suitability. We only considered studies that collected data under control (defined as absence of boats) and treatment (defined as presence of boats) utilizing the same techniques in both cases. To minimize research disturbance on the animal, we analyzed studies that collected data from land and, in case of data collected from a research vessel, we included only those studies that evaluated the direct effect the research platform (see Lusseau 2004 for detailed descriptions of data collection). Based on the information provided in the protocols, we gave a subjective score ranging between bad, fair, good, very good and excellent (see Senigaglia et al. 2012b for details on protocol evaluation). Only studies ranking good to excellent were included in the analyses. We further contacted 16 research groups to obtained mean and SD data for the relevant variables.

Since responses to a disturbance stimulus may vary, we considered it important to examine a wide variety of metrics to quantify disturbance consequences. These included changes in activity budget (foraging, resting, travelling and socializing, as defined in Lusseau [2003]), respiration rates, and movement metrics (deviation, directness index and swimming speed). We estimated activity budgets from activity state transition matrices from focal group follows (Lusseau 2004). Respiration rates were calculated as the mean inter-breath interval (IBI) of an entire dive cycle, including both dive and surface, by dividing the number of breaths in a follow by the duration of the follow (expressed in minutes). We averaged the respiration rate across focal follows and among individuals. Deviation and directness index (DEVI and DIRI, respectively) were calculated following Williams et al. (2002) and were restricted between 0–180 and 0–100, respectively. DEVI and DIRI represented a measure of path predictability and sinuosity, respectively, with a value of 0 for DEVI indicating predictable, straight movement, and a value of 0 for DIRI representing a circular path. Swimming speed was measured in meters per hour and was averaged across encounters. To model the effect of ecological condition, we divided the habitats by range type (feeding ground, breeding ground or residency) and by presence (official or voluntary) or absence of whale-watching regulations. Additionally, we looked at differences between the 2 suborders and coarsely assumed all mysticetes to be solitary and migratory while all odontocetes to live in social groups and be fairly resident all year round. The lack of a notable amount of replicates per species prevented us from using species itself as the explanatory variable.

Meta-analyses

We conducted meta-analytical regression to assess the variability in effect size across studies, using the package metafor (Viechtbauer 2010) in R ver. 2.11.0 (R Core Development Team 2010). We grouped the studies by the variables used to evaluate whale-watching effects. We fitted the meta-analytical model using the calculated effect sizes as the response variable and we fitted random effect models assuming variation in the true effect of whale-watching across studies. The null hypothesis was that the effect size was independent from whale-watching presence. The response variables are to some extend correlated but the strength of using multiple proxies for disturbance is the possibility to identify which one is the most sensitive indicator.

The factors influencing the response variables were included in the model as moderators (covariates) and we estimated their influence on the mean of the true effect and its associated variance. The included moderators were: suborder (whether belonging to mysticetes or odontocetes, assuming differences in social characteristics and life history strategies among the 2 suborders), the presence of whale-watching regulations (official, voluntary, or absent) and the habitat type (breeding, feeding

[1]MARMAM is a public mailing list dedicated to marine mammals research and management. At 2010 it counted more than 8500 subscribers

ground, or resident). In addition we included body size as moderator within activity budgets models and used it as a crude estimate of metabolic requirements. We considered the possibility of conducting a multivariate analysis, but it was not possible because not every study measured all variables.

Estimates of effect size

To examine whale-watching effects on inter-breath interval and movement metrics (DIRI, DEVI, and speed), we calculated their standardized mean difference (SMD) in the presence and absence of whale-watching vessels and used it as the outcome measure. SMD was calculated as the mean difference divided by the pooled SD of the groups (Viechtbauer 2010). To examine changes in the activity budget caused by whale-watching interactions, we calculated the log odds ratio between impact and control situation for each study and activity state. This measure represented the probability of a particular activity to occur during control (absence of whale-watching boats) compared to impact situations (presence of whale-watching boats), while accounting for differences in sample size. We used the log odds ratio values as a response variable and fitted a model for each activity state using restricted maximum-likelihood to minimize bias and to increase computing efficiency (Viechtbauer 2010). We compared the different models using Akaike Information Criteria (AIC).

RESULTS

We received and analyzed data from 15 different studies (1 study examining 2 separate populations, Table 1), in line with other meta-analyses on disturbance response (Stankowich 2008), of which 8 studies examined changes in activity budget, 6 considered variations in inter-breath intervals, 6 measured speed, and 5 explored differences in deviation and directness indices (Table 1). All meta-analyses showed high levels of heterogeneity in the direction and magnitude of the measured effects, and different metrics were influenced by different moderators (Table 2).

Results showed that variations in path sinuosity, represented by the deviation index, appropriately captured cetacean disturbance response. The model indicates an increase in path sinuosity in response to whale-watching disturbance consistent across studies: (tau^2 = 0.09, β = 0.34, p-value = 0.0001, k = 5; where tau^2 is the among-study variance, assessing consistency across studies, β is the effect size, and k is the number of studies compared in the meta-analysis). We found no evidence for an effect of the tested moderators on the variation of the deviation index, and the null model (i.e. no effect) was the best fit according to the AIC value (Table 2). Thus, based on the variables considered, the total variability in the effect size estimates was predominantly due to heterogeneity among the studies.

Although related to deviation index, changes in directness index, due to vessel presence, were not consistent across studies. However, most of the studies showed a decrease in path linearity (decreased value of directness index) in the presence of a whale-watching boat. Differences in the directness index were significantly influenced by habitat type that accounted for as much as 71% of the total heterogeneity (tau^2 = 0.05, QE = 3.12, p-value = 0.08, k = 5; where QE is the test for residual heterogeneity after the inclusion of a moderator, p-value refers to QE). In particular, path linearity decreased on breeding grounds (Table 2) but increased in corridor habitat type (Table 2).

Despite the detection of changes in speed due to whale-watching presence in Iceland, New Zealand, and Argentina, most of the variation in the effect size estimates was attributed to heterogeneity among the true effects (tau^2 = 0.031, k = 6, β = 0.01, p-value = 0.8). The model without moderators had the best fit according to the AIC value (Table 2). Speed significantly increased where regulations were in place (β = 0.27, p = 0.08) but the response was variable across species. For instance, right whales *Eubalaena australis* in Argentina increased their mean swimming speed, while humpback whales *Megaptera novaeangliae* in New Caledonia and dusky dolphins *Lagenorhynchus obscurus* in New Zealand decreased their mean swimming speed during whale-watching interactions.

Inter-breath intervals were not significantly influenced by whale-watching presence, and the type and intensity of the responses were study-specific. During whale-watching encounters, minke whales *Balenoptera acutorostrata* in Iceland and humpback whales in Australia significantly decreased their inter-breath intervals, while killer whales *Orcinus orca* in Haro Strait, USA and bottlenose dolphin *Tursiops truncatus* in New Zealand significantly increased their inter-breath intervals (Fig. 1). According to AIC values, the best-fit model included no moderators (tau^2 = 0.035, β = –0.002, p-value = 0.9,

Table 1. Summary of data provided by each study included in the meta-analyses: the contributor's name (as it appears in Figs. 1 & 2) and the study reference, the suborders and the species targeted, habitat type (winter ground = feeding ground in which researchers observed mating behavior confirmed by progesterone analyses and calving), location of the study, and the presence of whale-watching approach regulations (Reg) during the time the study was conducted (Yes = regulations in place, No = regulations not in place, V = presence of voluntary code of conduct during the time the study was conducted). DevI = deviation index; DirI = directness index; IBI = inter-breath intervals. Abbreviated species names given in parenthesis: Ba = *Balenoptera acutorostrata*; Mn = *Megaptera novaeangliae*; Ea = *Eubalaena australis*; Bm = *Balaenoptera musculus*; Ta = *Tursiops aduncus*; Tt = *Tursiops truncatus*; Lo = *Lagenorhynchus obscurus*; Oo = *Orcinus orca*; Ch = *Cephalorhynchus hectori*; Dd = *Delphinus delphis*

Name	Study	Suborder	Species	Habitat	Site	Reg	DevI	DirI	IBI	Speed	Activity budget
Bejder	Bejder et al. (2006a)	Odontocetes	Indo-pacific bottlenose dolphin (Ta)	Resident	Australia						✓
Christiansen	Christiansen et al. (2013a)	Mysticetes	Minke whale (Ba)	Feeding ground	Iceland	No	✓	✓	✓		
Christiansen2	Christiansen et al. (2010)	Odontocetes	Indo-pacific bottlenose dolphin (Ta)	Resident	Zanzibar	No					✓
Gendron	Gendron et al. (2012)	Mysticetes	Blue whale (Bm)	Winter ground	Mexico	Yes			✓		
Lundquist	Lundquist et al. (2013)	Mysticetes	Right whale (Ea)	Breeding ground	Argentina	Yes	✓	✓		✓	
Lundquist2	Lundquist et al. (2012)	Odontocetes	Dusky dolphins (Lo)	Resident	New Zealand	V	✓	✓		✓	
Lusseau	Lusseau (2004)	Odontocetes	Bottlenose dolphin (Tt)	Resident	New Zealand	Yes			✓		✓✓[a]
Lusseau2	Lusseau et al. (2009)	Odontocetes	Southern killer whales (Oo)	Resident	USA	V					✓
Martinez	Martinez et al. (2010)	Odontocetes	Hector's dolphin (Ch)	Resident	New Zealand	Yes					✓
Noren	Noren et al. (2009)	Odontocetes	Southern killer whales (Oo)	Resident	USA	V				✓	
Schaffar	Schaffar & Garrigue (2008)	Mysticetes	Humpback whale (Mn)	Migratory corridor	New Caledonia	V	✓	✓	✓	✓	
Stockin	Stockin et al. (2008)	Odontocetes	Common dolphin (Dd)	Resident	New Zealand	Yes					✓
Williams	Williams et al. (2006)	Odontocetes	Northern killer whales (Oo)	Resident	Canada	Yes					✓
Smith[b]	Williams et al. (2009)	Odontocetes	Southern killer whales (Oo)	Resident	USA	V	✓	✓	✓	✓	
Smith2	Smith (2008)	Mysticetes	Humpback whale (Mn)	Migratory corridor	Australia	Yes			✓	✓	

[a]Within the same study, data on activity budget have been collected for 2 separate populations of bottlenose dolphins in New Zealand. We considered them as 2 independent data points in our analysis

[b]Data were collected and provided by co-author J. C. Smith of the Williams et al. (2009) study

Table 2. Models developed in meta-regression analyses. k = number of studies compared in the meta-analyses (per metric), tau^2 = estimate of the total amount of heterogeneity (variance within studies plus the variance between studies), β = effect size, SE = standard error associated with β (*$p < 0.05$). Akaike's Information Criterion (AIC) values were used to compare models (smaller AIC values indicate a better model fit; the smallest AIC value of a category is shown in **bold**). Models contain different studies since not every study measured the same variables. Thus, within moderator levels may vary; for example, there are no studies analyzing speed variations on feeding ground. Further heterogeneity results are also given: Q = test for heterogeneity, QE = test for residual heterogeneity after the inclusion of a moderator, p-value = significance value for either Q or QE, nd = not determined, cells blank where test not applicable. Suborder M and O denote mysticetes and odontocetes, respectively. See Table 1 for details on regulation and habitat

Model Moderator	k	tau^2	β	SE	Q	QE	p-value	AIC
Deviation Index	5	0.09	0.34	0.15	24.63	nd	<0.0001	**7.03**
Suborder M	5	0.12	0.38	0.23	nd	19.4	<0.001	9.19
Suborder O			0.30	0.36				
Regulation YES	5	0.15	0.55	0.52	nd	9.50	<0.001	10.63
Regulation NO			0.19	0.40				
Regulation V			0.30	0.50				
Habitat breeding ground	5	0.12	0.78*	0.39	nd	6.41	0.01	10.95
Habitat corridor			0.004	0.67				
Habitat feeding ground			0.10	0.53				
Habitat resident			0.30	0.47				
Directness Index	5	0.17	−0.19	0.20	31.96	nd	<0.0001	10.72
Suborder M	5	0.32	−0.10	0.35	nd	15.3	<0.001	12.15
Suborder O			−0.23	0.55				
Regulation YES	5	0.51	0.14	0.90	nd	15.0	<0.001	12.68
Regulation NO			−0.42	0.71				
Regulation V			−0.22	0.88				
Habitat breeding ground	5	0.05	−0.54*	0.26	nd	3.12	0.08	**10.21**
Habitat corridor			1.01*	0.55				
Habitat feeding ground			−0.43	0.35				
Habitat resident			−0.19	0.32				
Speed	6	0.031	0.01	0.09	14.04	nd	0.01	**3.54**
Suborder M	6	0.036	0.08	0.14	nd	10.1	0.03	6.13
Suborder O			0.09	0.20				
Regulation YES	6	0.008	0.27	0.17	nd	6.5	0.16	3.92
Regulation V			−0.09	0.06				
Habitat type	6	0.023	0.31	0.21	nd	4.24	0.24	7.56
Habitat corridor			0.09	0.26				
Habitat resident			0.09	0.24				
Inter-breath interval	6	0.03	−0.002	0.09	138.5	nd	<0.0001	**7.09**
Suborder M	6	0.031	−0.09	0.10	nd	44.8	0.11	7.85
Suborder O			0.02	0.18				
Regulation YES	6	0.007	0.05*	0.11	nd	9.9	0.02	10.79
Regulation NO			−0.23*	0.09				
Regulation V			0.12*	0.12				
Habitat breeding ground	6	0.16	−0.25	0.33	nd	7.52	0.02	12.87
Habitat feeding ground			−0.23	0.51				
Habitat resident			0.23	0.44				
Habitat winter ground			0.03	0.52				
Behavioral budget-travelling	8	0.466	0.42	0.25	81.2	nd	<0.0001	**19.34**
Body size	8	0.55	0.49	0.15	nd	69.5	<0.0001	20.06
Behavioral budget-resting	8	0.44	−0.69	0.36	144.7	nd	<0.0001	**17.90**
Body size	7	0.79	−1.61*	0.68	nd	23.2	<0.001	20.24
Behavioral budget-foraging	8	0.30	−0.29	0.21	49.5	nd	<0.0001	**17.56**
Body size	8	0.33	0.41	0.13		49.5	<0.0001	17.89

k = 6). The model with suborder as moderator displayed the second best AIC value, with less than 1 unit difference from the first (Table 2) and should be taken into account; although the moderator was not statistically significant in itself (tau^2 = 0.031, QE = 44.8, p-value = 0.11, k = 6). Overall, mysticetes decreased inter-breath intervals when whale-watching boats were present, while odontocetes increased

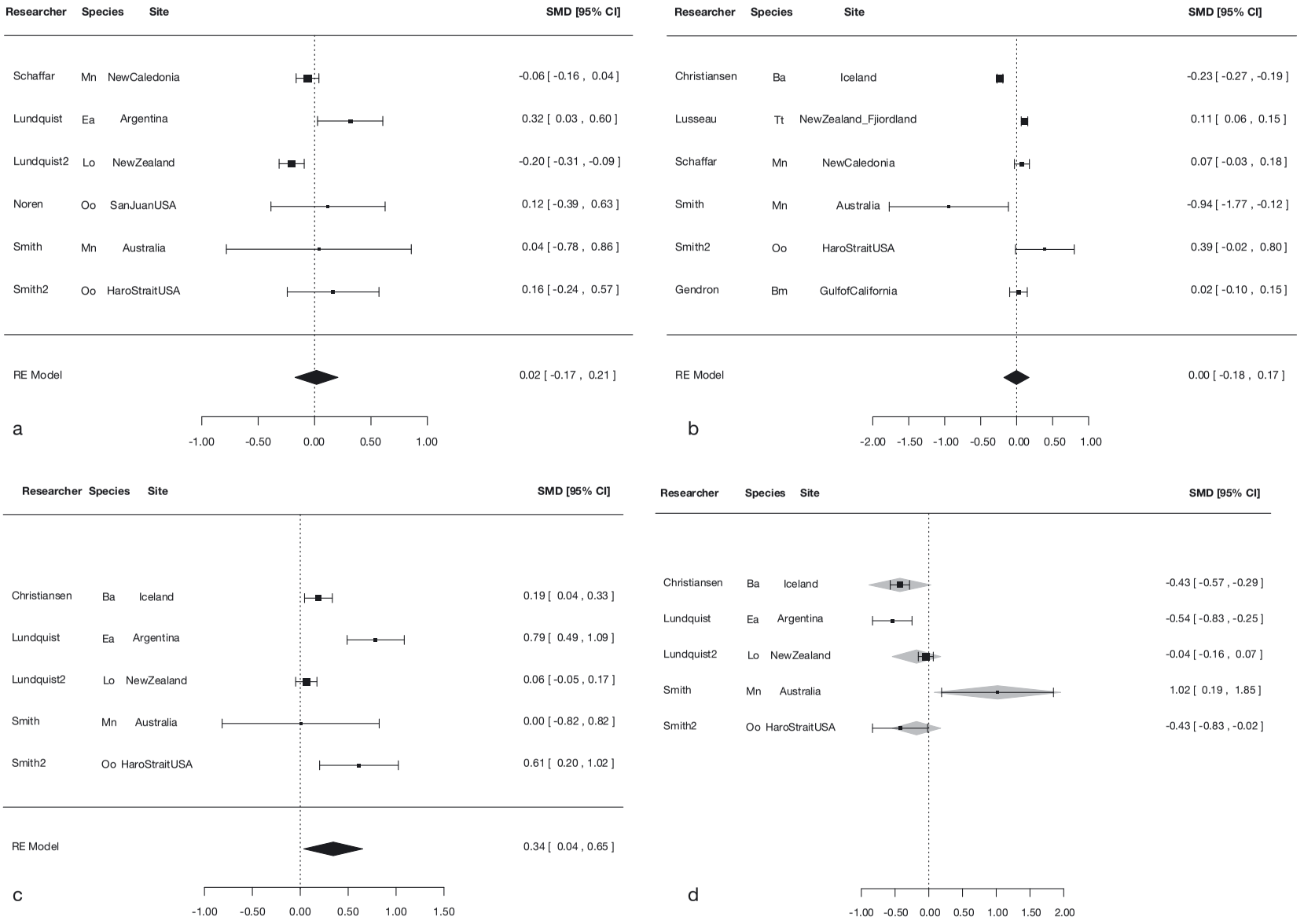

Fig. 1. Forest plot showing results for the 4 movement metrics (a) speed, (b) inter-breath interval, (c) deviation index, and (d) directness index. Study authors (see Table 1 for details), species, site, and standardized mean differences (SMD) values with their confidence intervals are shown (left-to-right). The dotted vertical line represents the line of no effect; a study crossing this line shows no significant effect of whale-watching presence. Positive deviation from zero (right of the line) and negative deviation from zero (left of the line) indicate a significant increase and decrease, respectively, of the response variable during whale-watching encounters. Dimension of the square representing each study is directly proportional to the sample size and hence the influence of the study within the meta-analysis. Black diamonds represent the overall effect of whale-watching presence on the metrics variations. The overall effect for directness index is not shown in the graph since part of the heterogeneity of the effect can be explained by the moderator habitat type (grey diamonds). RE model: random effects model without moderator

their inter-breath intervals (Table 2). Moreover, where regulations (voluntary or mandatory) were in place, inter-breath interval duration significantly increased (Table 2); this factor accounted for as much as 79% of the total heterogeneity.

Activity budgets significantly differed as a consequence of whale-watching presence in most of the studies. However, there was some heterogeneity across studies in the direction and magnitude of the responses (Fig. 2). Overall, during impact situations, animals were more likely to travel ($tau^2 = 0.466$, $\beta = 0.42$, p-value < 0.0001, k = 8) and less likely to rest ($tau^2 = 0.44$, $\beta = -0.69$, p-value = 0.0001, k = 7) and forage ($tau^2 = 0.30$, $\beta = -0.29$, p-value = 0.0001, k = 8). Bottlenose dolphins in New Zealand, on the contrary, significantly increased foraging time in the presence of whale-watching boats, however in this study, foraging was not distinguishable from vertical avoidance behavior (New et al. 2012). The presence of whale-watching boats also affected resting activity, with body size having a significant influence on the proportion of time spent resting ($tau^2 = 0.79$, $\beta = -1.61$, p-value < 0.001, k = 7); smaller species were generally less likely to rest in the presence of boats.

DISCUSSION

Our results show a wide array of responses to whale-watching boats with some similarities among studies. Changes in activity budget and path sinuosity were the most consistent metrics that captured heterogeneous cetacean responses to whale-watching disturbance. Despite some differences among species, both variables were significantly affected by whale-watching presence. On the contrary, changes in other movement metrics and inter-breath intervals were not homogeneous across studies. Our results further indicate that none of the tested explanatory variables was consistently significant across metrics and studies, suggesting that socio-ecological factors influence response behavior in a case specific manner. From a management perspective, it is particularly interesting that the presence of a regulatory code of conduct, whether official or voluntary, did not influence cetacean responses. The only exception was represented by variation in swimming speed; cetaceans varied their speed, in a case specific manner, when unregulated whale-watching boats were present. However, we have no further data on what the codes dictate nor on the level of observance by boats, thus we refrain from commenting on the general effectiveness of whale-watching codes of conduct.

Changes in swimming speed, deviation and directness index and inter-breathing intervals in the presence of whale-watching boats represent mechanistic responses to a disturbance stimulus. We expect mechanistic responses to vary among species due to physiological and ecological constraints. For instance, fast species with elongated bodies (e.g. Balaenopteridae), evolved to reduce drag and improve swimming efficiency, are likely to respond to vessels by increasing their speed of travel (Ford & Reeves 2008, Christiansen et al. 2014). In the same way, we expect smaller cetaceans to adopt different avoidance techniques due to physiological limitations, which do not allow them to outpace fast-moving whale-watching boats. While our results show a decrease in swimming speed of small dolphins (e.g. dusky dolphin) during whale-watching encounters, overall speed did not significantly change between impact and control situations. In contrast, findings from unpublished data by Weinrich et al. (2010) found a significant increase in humpback whale swimming speed in the presence of whale-watching boats. The authors suggested that mysticetes might suffer a small energetic cost due to high speed and thus favor fleeing as an evasive tactic.

In our study, however, there was no evidence supporting a preference of mysticetes for adopting this avoidance tactic, and the inclusion of the variable suborder was not significant in the model. Since body shape influences energetic costs, among mysticetes, species with elongated bodies (e.g. minke whales) may favor a different response compared to bulkier species like humpback whales (Ford & Reeves 2008). Thus, inter-species morphological differences might influence speed responses at a finer scale than a coarse distinction between mysticetes and odontocetes. It is also important to highlight, however, the consistency across studies of a significant increase in path sinuosity during whale-watching encounters. This response may reflect an attempt of the animals to avoid the boats without leaving the area (Christiansen et al. 2013a). In fact, trying to outpace a boat within a relatively confined area may lead to complete abandonment of a critically important area (Williams et al. 2002; Stankowich & Blumstein 2005). Related to deviation index, our results show a decrease in path linearity in presence of a whale-watching boat in all studies, except for humpback whales in Australia. Changes in directness index were influenced by habitat type, which characteristics can favor a more or less direct path in presence of whale-watching boat. To account for the importance

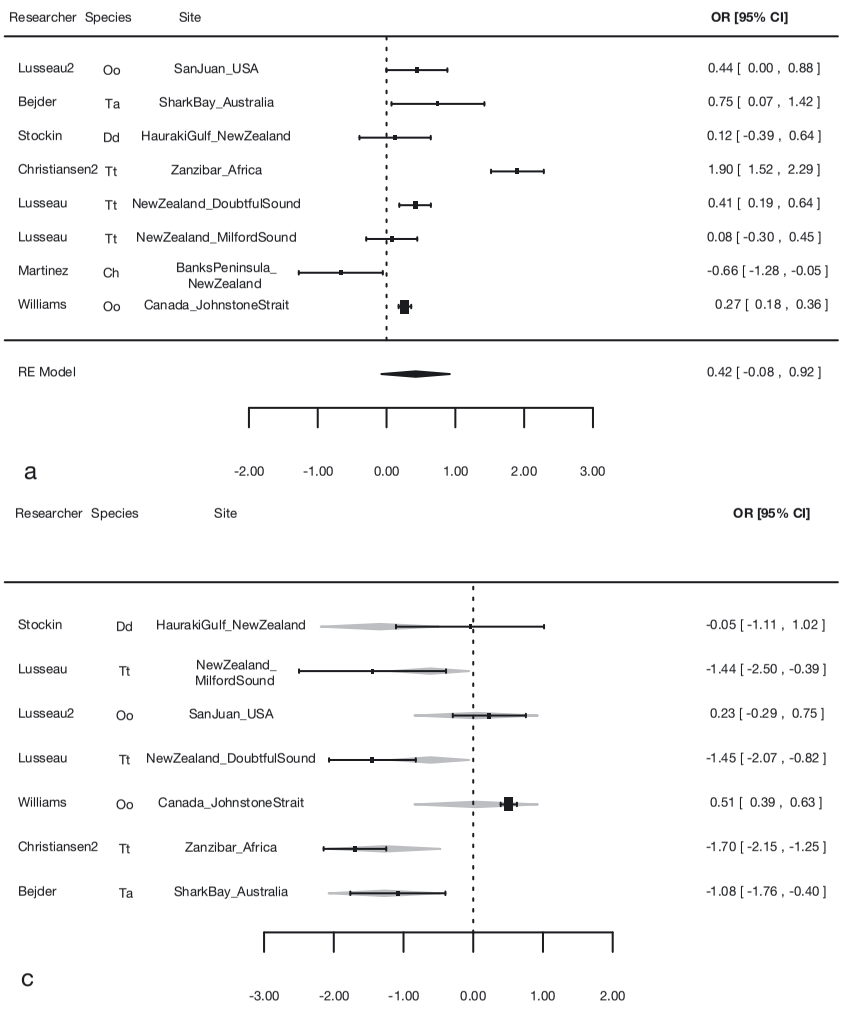

Fig. 2. Forest plot showing results for the meta-analyses of the activity budget, showing differences in (a) travelling, (b) foraging, and (c) resting activity during impact situations. Studies are ordered in an increasing order of time spent performing each activity in control situations. Values on the right are odds ratios (ORs) with 95% confidence intervals for each study. The dotted vertical line represents the line of no effect; a study crossing this line shows no correlation between variation in the response variable and whale-watching presence. Dimension of the square representing each study is directly proportional to the sample size and hence the influence of the study within the meta-analysis. Diamonds represent the estimated average log OR with associated 95% CI. In the case of resting, the estimated average log OR is not shown in the graph since part of the heterogeneity among effects can be explained by the moderator body size (grey diamonds). RE model: random effects model without moderator

of each study area, we added the type of habitat as an explanatory variable. However, this variable influenced only directness index and the paucity of studies from each habitat type prevented reliable conclusions from being drawn.

It was also important to consider the influence of social behavior on the type of disturbance responses and to reflect upon how disturbance can affect sociality. Whale-watching disturbance may lead to permanent social disruption by direct take of individuals due to boat collision, or temporary disruption by physical separation of the group that can occur due to the movement of boats, or due to different evasive and physiological constraints of individuals within the group (e.g. differences in swimming abilities between adults and calves, metabolic rates, personality)(Careau et al. 2008, Biro & Stamps 2010, Wade et al. 2012). These within group differences may cause the removal of more sensitive individuals affecting population parameters (Wade et al. 2012). Our comparison between mysticetes, considered mostly solitary, and odontocetes, considered largely social, highlighted some differences in swimming speed that can be explained by physiological constraints. Overall, however, the variable suborder did not appear to affect the type of response to whale-watching vessels. The lack of influence of this variable may be due to our crude categorical distinction between mysticetes and odontocetes. Whale-watching disturbance may be equally negative for both suborders, since odontocetes are very socially complex animals and disrupting the communications between mysticetes or their groups could also be detrimental. Disruption of social behaviour should not be underestimated and a finer analysis on intra-population differences is necessary as it might reveal further insight on disturbance responses in social animals, as suggested by a few studies on odontocetes (Bejder et al. 2006a, Williams et al. 2006, Senigaglia et al. 2011, 2012a).

Perhaps more relevant for the long-term sustainability of the industry were the measured changes in activity budgets, which may lead to energetic unbalance and have been shown to affect population dynamics in some odontocetes species (Bejder et al. 2006a,b). Significant changes in activity budget occurred in most of the studies included in the present meta-analysis. Despite some inter-study differences, the direction of the response (whether the log odds ratio of the examined activity state increased or decreased under disturbance conditions) was fairly consistent and involved more time spent travelling and less time allocated to resting when whale-watching boats were present. These results, combined with longer and more convoluted trajectories adopted to avoid boats, suggest a greater energetic expenditure along with shorter recovery periods. An increase in energetic requirement may be trivial for animals if food is largely available and energetic balance can be readily re-established. However, in food limited conditions (e.g. Southern Resident Killer Whales) (Williams et al. 2011), the population's ability to buffer this cost is low. Moreover, avoidance responses may carry additional costs if calves are present. For instance, the energetic expenditure is greater for adults swimming with calves in echelon position (Williams & Noren 2009). In this case, avoiding boats by increasing speed may be energetically too demanding. Also, since nursing usually occurs during resting periods, disturbance may potentially reduce nursing time (Bejder et al. 2006b, Stensland & Berggren 2007). This risk would be higher if the disturbance occurs on breeding grounds or during a delineated breeding period.

Some data were not available for every study, which prevented us from conducting an in-depth analyses of whale-watching disturbance and these limitations should be taken into account. For instance, we defined disturbance as the presence of whale-watching boats, regardless of their actual numbers. However, whales probably perceive disturbance along a context-specific spectrum and consequently adapt their responses. An oversimplification of disturbance may have confounded some results. If animals react adopting opposite tactics to different level of disturbance (e.g. few or many boats), taking the average may mask the actual response, which could have happened in some of the considered studies (Williams & Ashe 2007). Thus, future research should look at boat number, proximity and vessel type. Another caveat of our analysis is the assumption of equal responses among sexes, age classes, and group composition that could have biased some of our results. However, because of the heterogeneity of cetacean responses and the logistical impediments to conduct long-term research, comparative studies are required to properly evaluate the effects of this industry on animals and their populations. Consequently, our results can be useful for improving inference from many small-scale studies and allow inferences about whale-watching disturbance in cases where managers must make evidence-based decisions based on short-term, correlative studies, with small sample size or inadequate experimental controls.

CONCLUSIONS

To develop a predictive model on responses to disturbance, 3 factors should be evaluated: (1) multiple indicators of disturbance, (2) degree of interspecific variability, and (3) ecological factors and life history characteristics that could influence behavioral responses (Blumstein et al. 2005). We conducted the first meta-analysis of whale-watching studies covering these 3 factors and we found that changes in deviation index and behavioral budget reliably capture heterogeneous short-term cetacean responses to whale-watching boats across multiple species and locations. Our results should, however, be considered preliminary due to the paucity of suitable studies used in the analyses. For this reason, we recommend publishing guidelines for conducting and reporting whale-watching effect studies; this would ensure consistency and allow comparability. Some general guidelines are already available at the Large-scale Whalewatching Experiment (LaWE) website (https://sites.google.com/site/lawescience). We also encourage scientists to make data more readily available within the International Whaling Commission (IWC)/LaWE umbrella that can act as a depository library while ensuring that the intellectual property rights are respected. Data sharing would allow more detailed analyses.

None of the tested explanatory variables consistently influenced response behaviors in the presence of whale-watching boats. Since presence of regulatory measures of the industry did not consistently relate to response behaviors, further studies testing their case-specific efficacy should be conducted. There also remains a knowledge gap in the evaluation of long-term impacts on demographic parameters. The likelihood that behavioral disruptions will affect the fitness of individuals depends on their ability to compensate and varies accordingly to specific ecological and social conditions (New et al. 2012). Future studies should also address population specific differences to evaluate long-term impact of whale-watching activities, which are important to ensure the sustainability of this industry.

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