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Behavioural effects of whale-watching activities on an Endangered population of humpback whales wintering in New Caledonia

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ABSTRACT: After decades of whaling, Oceania humpback whales *Megaptera novaeangliae* have such a low rate of recovery that a trend is not currently measurable. They are listed as Endangered by the IUCN, and any possible threat to the whales needs to be carefully monitored and mitigated. Whale-watching activities represent an important economic development throughout the South Pacific but also carry a potential risk of impact for these recovering populations. New Caledonia is among the leading countries for humpback whale watching in Oceania. Land-based theodolite observations were conducted between 2005 and 2007 to assess the effect of boats on humpback whale behaviour in New Caledonia. Natural experiments were used to investigate the response of whales to boat approaches, and opportunistic observations were used to assess which variables best described variability in behaviour. Over 80% of whales approached by boats significantly changed their behaviour. Changes in path predictability (directness and deviation index) were most commonly affected and are likely to represent an efficient and low-cost avoidance strategy. Linear models showed that as boats get closer, humpback whales significantly increased the sinuosity of their path. The threshold for such a response corresponded to an approach distance of 335 m. Based on these results and considering the vulnerability of the humpback whale population in New Caledonia, we suggest reinforcing management measures to increase the likelihood that the whale-watching industry is sustainable.

KEY WORDS: Whale watching · Behavioural response · Disturbance · Sustainability · Management · Conservation

INTRODUCTION

Over the last 2 centuries, Southern Hemisphere humpback whales *Megaptera novaeangliae* were extensively hunted, reducing populations to a few percent of their pre-exploitation abundance (Chapman 1974). Clapham & Baker (2002) estimated that over 200000 Southern Hemisphere humpback whales were killed during commercial whaling operations conducted between 1904 and 1980. Although these whales were ostensibly protected from commercial whaling by the International Whaling Commission (IWC) in 1966, illegal kills by the Soviet Union continued until 1972 (Clapham & Ivashchenko 2009). This led to a population crash of humpback whales in several areas, including south of Australia, New Zealand and the South Pacific Ocean (Clapham et al. 2009). Today, in contrast with other stocks, Oceania humpback whales are recovering very slowly and are estimated at approximately 25% of their pre-whaling abundance (Constantine et al. 2012). As a result, Ocea-

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nia humpback whales were listed as Endangered in 2008 (IUCN 2008).

The South Pacific Regional Environment Programme therefore considers threat reduction as a priority for this stock (SPREP 2007). Humpback whales wintering in New Caledonian waters represent one of the smallest populations within Oceania, with only 327 individuals (coefficient of variation = 0.11; Garrigue et al. 2004). Strong site fidelity (Garrigue et al. 2002), combined with demographic and reproductive isolation (Garrigue et al. 2004, Olavarría et al. 2007), suggests that any threats on their breeding ground may further affect their recovery.

In recent years, watching whales in their natural habitat has developed as a valuable economic alternative to whaling (Hoyt 2001, O'Connor et al. 2009) and an important educational tool to raise public awareness of the need for species and habitat protection (Hoyt 2001). But without appropriate management, the presence of boats around cetaceans can induce behavioural changes (e.g. Corkeron 1995, Sousa-Lima et al. 2002, Williams et al. 2002, Constantine et al. 2004, Foote et al. 2004, Scheidat et al. 2004, Christiansen et al. 2010), and can therefore represent a threat to the species exposed (IFAW 1999, Corkeron 2004). Some of these behavioural responses may carry energetic costs to individuals (Williams et al. 2006) and cumulatively may have population-level effects (e.g. Bejder et al. 2006a). To date, most of these studies have been conducted on odontocetes, and studies on the impact of whale watching on mysticetes are scarce.

Following the worldwide trend, the whale-watching industry throughout the South Pacific Islands region has demonstrated a remarkable growth of 45% per annum since 1992 (Economists At Large 2008). In particular, humpback whales, migrating every winter from Antarctica to their tropical breeding grounds, attract thousands of tourists and are the most popular species for tourism in the region (Orams 1999, Schaffar & Garrigue 2007, Economists At Large 2008). These small populations may be particularly at risk whilst on their breeding grounds, but quantitative data on the effects of tourism on the endangered Oceania humpback whales are lacking. Since humpback whales fast during migration and on their breeding grounds, they are limited in their ability to compensate for energetic costs potentially caused by a disturbance. If sufficiently high, these energetic costs could lead to females having to redirect energy from lactation to homeostasis for survival, which could affect their long-term reproductive success.

New Caledonia is one of the leading boat-based whale-watch destinations in the South Pacific region (Schaffar & Garrigue 2007, Economists At Large 2008, Schaffar et al. 2010). Since its inception in 1995, this industry has had an average annual growth rate of 40% and involved 26 tour operators in 2008 (unpubl. data). Considering the small number of humpback whales wintering in New Caledonia and their slow recovery from past whaling operations, the growth of whale-watching activities and the absence of management measures at the time of the study raised the question of the potential impact the presence of boats may have on the whales. A study was initiated in 2005 to assess the behavioural responses of humpback whales to commercial and recreational whale-watching boats, and to identify factors that may influence such responses. This study also aimed at identifying the level of the explanatory variables likely to lead to a significant change in the whales' behaviour. Information on factors affecting cetacean behaviour is critical to ensure that management measures are adapted to each population and are indeed efficient at minimising the impact of human activities (Noren et al. 2009).

MATERIALS AND METHODS

Data collection

Between mid-July and mid-September 2005 to 2007, observations were made from Cap Ndoua. This lookout point is located 189 m above sea level overlooking the southern lagoon of New Caledonia, a vast and open area with waters reaching up to 80 m in depth (Fig. 1).

Observations were conducted by a team of 3 researchers and took place from early morning (around 07:00 h) to mid-afternoon (around 15:00 h) during the time of year when humpback whales are present in the southern lagoon of New Caledonia (July to September). Observations were restricted to days with no rain and a wind speed less than 15 knots.

A Sokkia Set 5 theodolite was used to monitor the movement and behaviour of humpback whales in the absence and presence of boats. The theodolite was connected to a laptop computer running the tracking program 'Cyclops' (www.cyclops-tracker.com). This program automatically transformed the vertical and horizontal coordinates from the theodolite readings into GPS points, and was used to record behavioural and fix data (i.e. whale breaths, boat identity), which

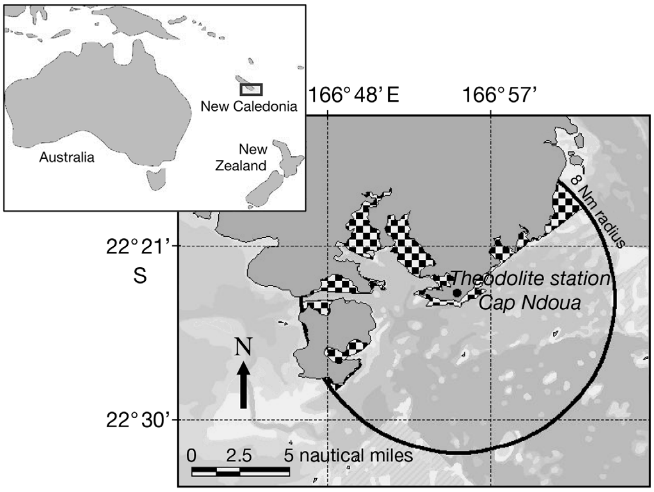

Fig. 1. Observation site and study area (limited to 8 nautical miles from the theodolite station to maximise tracking accuracy). The checked areas cannot be observed from the shore station

were verbally relayed by the theodolite operator to the computer operator. In order to minimise interobserver variability, the same person (A.S.) operated the theodolite for all days of this study.

Comparison of data collected from the land-based station and from boat-based surveys on the same groups of whales showed overlapping tracks and behaviours up to 8 nautical miles (n miles) from the lookout point on clear days and with a wind speed less than 5 knots. The maximum distance at which humpback whale groups were tracked was therefore set at 8 n miles. When weather conditions worsened, it was reduced to a distance where the blows and the backs of the animals could still be clearly seen.

The sighting rate of unique humpback whale groups within the study area remained relatively low with an average of only 1.8 groups d^{-1} between 2005 and 2007 (Schaffar et al. 2010). The low number of groups sighted reduced the likelihood of re-sampling the same group multiple times per day (pseudoreplication), and the choice of which group to track was limited. When more than 1 group was within sight of the land-based station, the group closest to shore was tracked. This choice was made to increase the probability of observing the group with boats afterwards. Because group composition on breeding grounds is highly unstable, the likelihood of re-sampling the same groups from one day to the next was considered limited, although the validity of this assumption could not be tested.

Samples of the whales' movements and behaviour, hereafter referred to as tracks, were included for analysis when there were at least 5 surfacing bouts combined with a minimum of 20 min of observation, but lasted as long as required to obtain the 5 bouts. These tracks allowed a representative sample of the whales' behaviour to be obtained. During tracks, the whales' position was fixed with the theodolite once every minute. The fix was taken on the first adult whale to come to the surface after that time elapsed. We considered a group of whales to be 1 or more whales within 100 m of each other, generally moving in the same direction in a coordinated manner (Whitehead 1983, Mobley & Herman 1985). Group type was recorded at the start of each tracking session. Four categories of group type were used: singleton, pair of adult whales, groups of 3 or more adults and groups containing a mother–calf pair (alone or accompanied by 1 or several escorts). A calf was defined as an animal in close proximity to an adult whale and visually estimated to be less than 50% of the length of the accompanying animal (Chittleborough 1965).

If boats were present or arrived specifically to watch the whales within a 1000 m radius of the group being tracked, their position was recorded between each fix of the group's position. An observer tracked the whales' behaviour while the theodolite operator fixed the position of boats.

Data preparation

Tracking sessions within which group type changed (i.e. affiliation or disaffiliation of individuals) were removed from the analyses. Theodolite tracks were then divided into 2 categories: (1) Natural experiments, in which focal groups entered the study area unaccompanied by boats and were monitored as boats approached (i.e. allowing a Before–During comparison of the whales' behaviour). (2) Opportunistic observations, in which focal groups were exclusively tracked with boats present within 1000 m.

Humpback whale groups exclusively tracked without boats present within 1000 m were excluded from the dataset.

The minimum distance of each boat to the group and the maximum number of boats present within 1000 m of the group were estimated for each whale position fixed with the theodolite. Based on these data, the mean number of boats present and the mean distance of approach were obtained for each tracking session.

Four behavioural response variables were considered: (1) Dive time: the time spent by whales underwater between each blow. The whales' dive time was calculated by selecting the longest dive times between 2 fixes and averaging these values for each tracking session. When blows could not be reliably recorded, dive intervals were removed from the data set. (2) Swim speed: the whales' net movement from one fix to the next, as underwater changes in swimming patterns were not studied. The mean swim speed was obtained by averaging the speed given by 'Cyclops' for each whale position fixed with the theodolite throughout a tracking session. (3) Directness index: the path predictability of the whales over the length of the tracking session. The straight-line distance between the first and the last fix of a tracking session was divided by the cumulative surface distance covered by the group (Williams et al. 2002). It ranges from 0 (circular path) to 1 (straight line). (4) Deviation index: the change in the whale's course (angle between observations) over 1 minute. The deviation index was obtained by averaging the re-orientation rate given by 'Cyclops' for each whale position fixed with the theodolite throughout a tracking session.

These variables correspond to the behaviour of cetaceans commonly tested to assess the short-term impact of whale-watching activities (Williams et al. 2002, 2009, Bejder & Samuels 2003, Scheidat et al. 2004, Morete et al. 2007, Stamation et al. 2010) and can be recorded from a shore-based station for humpback whale research.

The directness index was arcsine transformed, and the deviation index and dive time data were log-transformed for data analysis.

Natural experiments

In order to assess whether humpback whales changed their behaviour upon the arrival of boats within 1000 m of the group, data from natural experiments, i.e. when the same group of whales had been tracked both before and during the presence of boats, were used. Each group served as its own control, as it was first tracked in the absence of boats, reducing the probability that changes in behaviour could be linked to natural variability. Paired *t*-tests with known variance at the 95% level of confidence (i.e. $\alpha = 0.05$), which allow the comparison of means on the same subject in differing circumstances (McDonald 2009), were used to assess the difference of each of the 4 response variables considered in this study before boats arrived and during the presence of boats. The mean dive time, swim speed, deviation and directness indexes calculated in the 'before boats' and 'during interactions with boats' conditions were therefore compared using paired *t*-tests for each of the groups tracked during natural experiments.

Because group composition may affect whales' behaviour, 2-proportion *z*-tests were performed to assess whether group types differed in their response to the presence of boats. Such tests allow the comparison of 2 proportions created by 2 subgroups of 1 random sample (McDonald 2009). The proportion of each group type showing a significant change in behaviour upon the arrival of boats was compared for each of the 4 response variables considered in this study. Groups of 3 or more adult whales were not included in this analysis due to a small sample size (n = 2).

Opportunistic observations

Based on the opportunistic dataset, i.e. humpback whale groups tracked exclusively with boats, multiple linear models (LMs) were used to assess the relationship between the presence of boats and the whales' behaviour. This analysis allows modelling of the relationship between a response variable and several explanatory variables (McDonald 2009).

The response variables considered in these models were the whales' swim speed, dive time, directness and deviation index. The maximum number of boats present within 1000 m of the whales and the minimum distance of approach between whales and boats obtained for each track were considered as explanatory variables for this analysis. Maximum boat number and minimum distance of approach were selected as these represent measurable factors which are most commonly restricted in whale-watching guidelines and regulations worldwide (Carlson 2009). Group type was also included as an explanatory variable. The effect of other variables that may affect whale behaviour such as biological parameters, or other threats such as predation risk, could not be tested in this study, as data on these factors are not currently available for this population.

The response variables Y_i, were modelled as a function of the explanatory variables:

$$Y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \varepsilon_i \quad (1)$$

where the observations $i = 1,\ldots,n$ are independent; β_0, β_1, β_2 are the coefficients of variation corresponding to the explanatory variables x_{1i} and x_{2i}, i.e. boat number and boat proximity; and ε_i are the errors, normally distributed.

Diagnostic plots, i.e. histograms of residual distributions, normal QQ plots and plots of residuals versus fitted values, were also used to test the model assumptions and did not reveal any violation of these assumptions. A confidence level of 95% (i.e. $\alpha = 0.05$) was used in all analyses.

The Akaike Information Criterion (AIC) was used to determine models representing the best fit to the data (lowest AIC). Models with $\Delta AIC \leq 2$ were considered of equal value (Burnham & Anderson 2002).

Behavioural threshold

Identifying the level of the explanatory variables (e.g. boat number and distance of approach) potentially changing the whales' behaviour could inform management and minimise the impact of whale watching. Towards that goal, we developed an intuitive ad hoc method to identify the value of an environmental stressor over which a significant change in behaviour can be expected.

In our application and to be conservative, we used the presence of boats as the environmental stressor and behavioural variables for groups of whales not showing any significant change in behaviour based on the results of the paired *t*-tests. We expected the behavioural response to the environmental stressor to occur somewhere above the average of the behavioural variable before the arrival of the boats. More precisely, we used the averaged percentage of change in the behavioural variable before and during boat presence to identify this threshold such that:

$$\text{Behavioural threshold} = \bar{x}_{\text{before}} + \frac{\bar{x}_{\text{during}} - \bar{x}_{\text{before}}}{|\bar{x}_{\text{before}}|} \times 100 \quad (2)$$

where $\bar{x}_{\text{before}}$ is the mean of the response variable before the arrival of boats, and $\bar{x}_{\text{during}}$ is the mean of the response variable during the presence of boats.

The second step in identifying the level of the explanatory variables (i.e. boat number and boat proximity) potentially affecting whale behaviour was to use the threshold value with the results of the LMs to perform an inverse prediction. Using the best fitted model describing a significant relationship, values of the explanatory variable corresponding to the threshold of the response variable and associated 95% confidence intervals were calculated using the function 'inverse.Predict().'available in the R statistical package chemCal{}.

RESULTS

Research effort and sample size

Data were collected over 3 field seasons from 2005 to 2007 (Table 1). In total, 146 d were spent in the field, with a total of 873 h of observations.

A total of 175 groups were tracked using the theodolite, of which 72 were selected for the analysis. A total of 25 groups tracked both before and during boat interactions made up the experimental dataset (Table 1). The opportunistic dataset included 47 tracks conducted on groups in the presence of boats within 1000 m of the whales (Table 1). Pairs and singletons were the groups with the highest representation in each dataset (Fig. 2).

Response of whales to the presence of boats: experimental data set

Paired *t*-tests showed that the majority of humpback whales (84%) significantly changed at least 1 of the 4 behavioural variables considered in this study when approached by boats. In the 'during interactions with boats' condition, most whales showed horizontal avoidance by significantly changing their directness index (60%), their deviation index (64%) and/or their swim speed (44%) (Table 2). Fewer groups (20%) showed vertical avoidance by significantly changing their dive time.

The response of whales to the arrival of boats within 1000 m of the group varied between individuals. Few whales (16%) responded by changing only one of the behavioural variables considered, and when this did occur, it was always a horizontal avoidance tactic. Humpback whales were most likely to combine 2 or 3 response strategies (respectively 32 and 36%) either by using different horizontal avoid-

Table 1. *Megaptera novaeangliae.* Sampling effort over the 3 yr of the study and number of humpback whale group tracks (with boats, before and during interactions with boats) included in the dataset. For other details of tracking conditions see 'Results: Research effort and sample size'

Observation period	Sampling effort Days (n)	Hours (n)	Groups tracked (n) With boats	Before & during interactions
14 Jul–4 Sep 2005	42	236	13	5
18 Jul–17 Sep 2006	51	329	18	8
12 Jul–19 Sep 2007	53	308	16	12
Total	146	873	47	25

ance tactics (71%) or by combining horizontal and vertical avoidance strategies (29%).

The results of the paired *t*-tests also allowed assessment of the extent of the behavioural changes in the presence of boats. The percentage of change in the 'during interactions with boats' condition was calculated for each of the 4 behavioural variables depending on whether the whales responded significantly to the arrival of boats (Table 2). The scale of significant change differed between variables. The deviation and directness indices, although they represented the behavioural variables most often significantly affected by the arrival of boats, showed the lowest percentage of change with an increase of 11% and a decrease of 9%, respectively. Most often the arrival of boats induced a small change in path predictability, with a less linear direction of travel (directness) and/or a more sinuous path (deviation). In comparison, swim speed and dive time were less often significantly affected by the arrival of boats, but when they were, the extent of the change was higher. With an average increase of 133% for swim speed and 56% for dive time (Table 2), humpback whales sometimes swam over twice as fast and/or increased their time underwater by half of that spent when boats were not present. Groups that did not respond significantly to the presence of boats showed very low average percentages of behavioural change in each of the 4 variables considered between the 'before boats' and 'during interactions with boats' conditions (i.e. ≤5%). The 2-proportion *z*-tests did not show any significant differences in the response to boats according to group type.

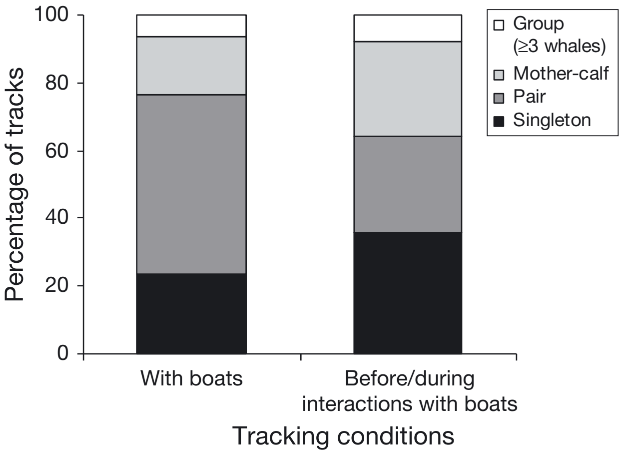

Fig. 2. *Megaptera novaeangliae.* Percentage of tracks conducted for each of the 4 group types considered in this study depending on the tracking condition (with boats, before and during interactions with boats). For other details of tracking conditions see 'Materials and methods: Data preparation'

Table 2. *Megaptera novaeangliae.* Changes observed upon the arrival of boats within 1000 m of humpback whale groups (n = 25) for each of the response variables considered in this study. Arrows represent a decrease or increase, respectively, of the response variable

Response variables	Groups showing significant change (%)	% of change (SE) and direction: Significant groups	Non-significant groups
Swim speed (knots)	44	133 (229) ↑	5 (28) ↑
Dive time (min)	20	56 (16) ↑	−3 (23) ↓
Directness index	60	−9 (16) ↓	1 (7) ↑
Deviation index (degree min^{-1})	64	11 (37) ↑	1 (9) ↑

Table 3. *Megaptera novaeangliae.* Akaike information criterion (AIC) values obtained for each of the 4 models tested. Lowest AIC values are in **bold**, and models leading to significant predictors are ticked (✓). Note that 3 points should be subtracted for dive time degrees of freedom (df) values, as a few data points had to be removed due to uncertainty.

Model	Explanatory variables	df	Directness index	Speed	Deviation index	Dive time
1	Number	1,45	**11.11**	**152.91**	109.97	**80.34**
2	Distance	1,45	**11.79**	**150.75**	**106.22**✓	**78.44**
3	Distance + number	2,44	**12.28**	**151.59**	**104.97**✓	**80.35**
4	Distance × number	3,43	14.15	153.34	**105.88**	81.01

Response of whales to the presence of boats: opportunistic data set

The results of the LMs showed that significant predictors could only be identified for the deviation index (Table 3). The maximum number of boats also contributed to models with low AIC but was never a significant predictor. Therefore, model 2 was considered a good compromise between simplicity and model fit for the deviation index. This model shows that the minimum distance of approach by boats significantly affects the whales' deviation index with an associated coefficient of −0.003. These results indicate that whales will have a more sinuous path as boats get closer. On average, the whales increased their turning angle from 2.87° to 5.97° (108%) when boats approached to a distance of between 300 and 100 m from the animals (Fig. 3).

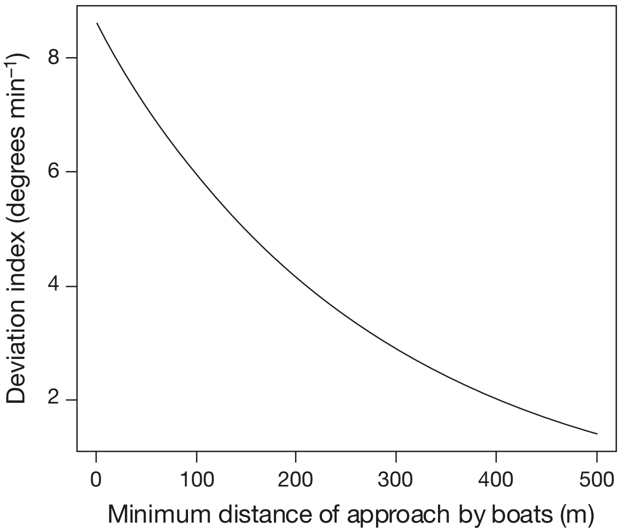

Fig. 3. *Megaptera novaeangliae.* Relationship between the minimum distance of approach by boats and humpback whale deviation indices with a coefficient of −0.003 as described by the linear model with the best fit (model 2 in Table 3)

Directness index, swim speed and dive time were not significantly affected by any of the explanatory variables analysed for the opportunistic data set (Table 3). Although group type was included in the LMs, it was not a significant predictor of the whales' behaviour nor did it lead to better fitting models.

Behavioural threshold

The threshold over which the behaviour of the whales is likely to correspond to a significant response to the presence of boats was obtained for the deviation index. The threshold is based on the back-transformed data available for groups from the natural experiment dataset that did not show significant changes in behaviour between the 'before boats' and 'during interactions with boats' conditions. Results show that a deviation index over 2.53° per minute is likely to be the result of a significant reaction to the presence of boats.

As model 2 for the deviation index shows that boats approaching whales at closer distances significantly increase the sinuosity of the animals' path, we estimated the distance at which boats were likely to cause a deviation index higher than the 2.53° per minute threshold using an inverse prediction calculation. Hence, the value of the explanatory variable corresponding to the threshold of the response variable equals:

$$[\ln(\text{behavioural threshold}) - x1]/x2 = [\ln(2.53) - 2.1536616]/-0.003658 = 335 \text{ m} \quad (3)$$

where $x1$ is the intercept value and $x2$ is the coefficient associated with the explanatory variable.

A deviation index of 2.53° per minute corresponds to a minimum distance of approach of 335 m (CI = 0; 798). Boats approaching whales at distances closer than 335 m are most likely to induce a significant increase in the sinuosity of the animals' path. The 95% confidence interval calculated indicates that the impact on the whales' deviation index could potentially be initiated as boats approach the whales closer than 798 m.

DISCUSSION

We have shown that whale-watching activities taking place in the southern lagoon of New Caledonia have a short-term impact on humpback whale behaviour. The majority (84%) of groups showed a significant change in at least one of the behavioural variables when boats were within 1000 m of the group. Even though the behavioural variables considered in this study could vary over time irrespective of boat presence or absence, we found that whales which did not react significantly to the presence of boats showed little change in behaviour. Therefore, it seems unlikely that the changes in behaviour identified in this study occurred randomly due to natural variability.

Humpback whales showed a strong preference for horizontal avoidance tactics in the presence of boats. These tactics were most commonly displayed in the presence of boats. When whales responded to boats by changing only 1 behavioural variable, they always used a horizontal avoidance tactic. Changes in deviation and directness were also most likely to be combined with each other than with a vertical avoidance tactic. More specifically, path predictability of the whales was most commonly affected by the presence of boats. Over 60% of groups significantly changed their deviation and/or directness index when approached by boats, and their swimming pattern became more erratic. These directional changes evoke the classic evasive tactics used by prey to avoid predators (Howland 1974, Weihs & Webb 1984, Frid & Dill 2002, Williams et al. 2002) and suggest that the presence of boats either represents a disturbance or is perceived as a threat that whales try to minimise. Such strategies are likely to be used as soon as approaching boats are detected, which could correspond to a distance greater than 1000 m (up to 4 km in Baker & Herman 1989).

Similar studies conducted on humpback whales and other cetacean species also report directional changes in the presence of boats, such as animals moving away from the approaching vessel (e.g. Baker & Herman 1989, Stamation et al. 2010) or displaying a more erratic path (e.g. Nowacek et al. 2001, Lundquist et al. 2008, Timmel et al. 2008, Williams et al. 2009).

Increases in swim speed and dive time have also been documented as a response to the presence of boats (e.g. Nowacek et al. 2001, Lusseau 2003, Scheidat et al. 2004, Morete et al. 2007, Lundquist et al. 2008, Timmel et al. 2008, Stamation et al. 2010). In the present study, such changes also occurred but were less frequent than directional changes. However, when they occurred, changes in net swim speed and dive time were of higher amplitude in comparison to the directness and deviation indexes. As the behavioural variables most affected by the presence of boats showed the lowest percentage of change, it seems possible that small changes in path predictability could be an efficient and low-cost strategy for humpback whales to avoid boats in New Caledonia. It also suggests that changes in swim speed and dive time may have to be of higher amplitude to be efficient, potentially representing a higher energetic cost for the animals, and therefore used as a secondary avoidance strategy. It seems unlikely that the lagoon settings influence these changes in behaviour, as escape routes are not limited by shallow and/or enclosed waters.

The analysis based on opportunistic observations showed that the minimum distance at which boats approach humpback whales in New Caledonia has a significant effect on the deviation index. The whale-watch guidelines implemented in New Caledonia in 2008 define the caution zone as the area within 100 to 300 m of a whale and recommend not approaching whales closer than 100 m (Province Sud 2008). The results of the present study show that when boats enter the caution zone and approach as close as 100 m from the animals, humpback whales are likely to increase the sinuosity of their path by over 100%. Neither the number of boats nor the type of group was identified as a significant predictor of the whales' behaviour. It seems likely that other factors that could not be accounted for in this study play a role in the response of whales to approaching boats (e.g. boat noise, angle and speed of approach, length of encounter, level of previous whale watch exposure) and may explain the changes in speed, dive time and directness index demonstrated in the analysis of the natural experiments. The calculation of a behavioural threshold allowed us to identify the level at which the deviation index of a whale exposed to boats is likely to correspond to boat presence. Based on this threshold and on the relationship between the minimum approach distance and the deviation index, it was possible to show that boats approaching within 335 m of the whales were most likely to induce a significant directional change. The confidence interval calculated for this value indicates that behavioural changes could already be initiated as boats approach within 800 m of the whales. In addition to adressing approach distances, the New Caledonian whale-watch guidelines also recommend for each boat to observe a group of whales for 1 h, and for each group of whales to be watched for a total cumulative time of 3 h d^{-1}. We suggest that extending the caution zone to 350 m and decreasing the time spent within 350 m of the whales would minimise the disturbance of whale-watching activities on humpback whales breeding in the southern lagoon of New Caledonia. Such revisions to the actual guidelines would allow a reduction in time during which the whales are exposed to boats each day. New Caledonia's whale watching industry has been well established for many years but lacks a management structure beneficial to both the industry and the whale population in the long term. Given the current situation, it seems unlikely that any measure further restraining tour operators could be implemented on a voluntary basis, especially given that not all New Caledonian whale-watching tour operators are signatories to the guidelines. Therefore, regulation of the existing guidelines combined with enforcement efforts via surveillance patrols is more likely to ensure compliance. With the small number of humpback whale groups in the study area and the increasing number of whale-watching boats operating daily, the implementation of a whale-watching licensing quota could also improve compliance of measures such as cumulative observation time.

Many questions about the potential long-term effects of whale watching on mysticetes remain. The only available study addressing the biological effects of boat exposure on large cetaceans did not find direct evidence for negative effects of whale-watch exposure on humpback whale calving rates and calf survival on their North Atlantic feeding ground (Weinrich & Corbelli 2009). The potential implications of whale-watch disturbance on breeding grounds could be different and are important to consider. Lactating females may be particularly at risk if they redirect energy from lactation to homeostasis in order to compensate for their own increased energy expenditure. This may compromise calf survival, as an increased energetic cost to the mother may affect lactation or gestation. Studies conducted on small cetaceans have shown that behavioural changes induced by the presence of only a few boats for short time periods can have population-level effects, especially if animals are repeatedly exposed to whale-watching activities (Bejder et al. 2006a,b, Lusseau & Bejder 2007).

Exposure to whale-watching activities for humpback whales in New Caledonia is likely to be limited to their residency time in the southern lagoon (maximum 60 d: Garrigue et al. 2001), but may be repeated over the years due to strong site fidelity (Garrigue et al. 2002). A study looking at potential changes in residency time could provide further information on the dynamics of this population with regards to the development of the whale-watching industry. It seems unlikely that the evasive tactics demonstrated in this study could lead to severe biological effects on the humpback whale population breeding in New Caledonia. However, we have shown that short-term disturbance from whale watching boats exists, and this should be considered by management authorities. The small number of humpback whales in New Caledonia combined with high site fidelity further warrants the implementation of management measures that will efficiently minimise any disturbance to this Endangered population.

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