

Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador

MEIKE SCHEIDAT*, CRISTINA CASTRO⁺, JANIRA GONZALEZ⁺ AND ROB WILLIAMS[#]

Contact e-mail: scheidat@ftz-west.uni-kiel.de

ABSTRACT

Machalilla National Park, on the coast of mainland Ecuador, supports a growing whalewatching industry that focuses on Southern Hemisphere humpback whales, which spend the austral winter (June–September) in this area. This study was designed to measure short-term reactions of whales to the whalewatching vessel activity typically seen in this area for two reasons: (1) to identify the nature of whales' avoidance response, if any, in order to draft whalewatching guidelines that help local mariners identify when they may be disturbing whales; and (2) to quantify the magnitude of any avoidance response, to examine how this relatively understudied population behaves around boats compared with whales in other whalewatching areas. A shore-based theodolite tracking team created a 'natural' experiment to observe relationships between whalewatching traffic and whale behaviour in 1998 and 1999. Swim speed and path directness of humpback whales were measured in the absence of boats, and how those parameters changed when boats arrived was recorded. When whales entered the study area accompanied by boats, a record was made of how their behaviour changed after the boats left. Humpback whales reacted to the approach of whalewatching boats by increasing swim speed significantly, and adopted a much more direct path after boats left. Future research is needed to determine whether responses vary with number, proximity or type of vessel. Similarly, future studies are recommended to determine whether different age-sex classes vary in vulnerability to disturbance. Meanwhile, this study enables provision of much-needed, practical advice to local operators who are concerned that they may be disturbing whales: one way that mariners can tell if they are causing disturbance is if they need to increase their vessel's speed to keep pace. The average behavioural responses measured were strong enough to recommend that Machalilla National Park adopt precautionary management procedures to limit number and proximity of vessels.

KEYWORDS: HUMPBACK WHALE, SOUTH AMERICA, WHALEWATCHING, BEHAVIOUR, SHORT-TERM CHANGE

INTRODUCTION

Researchers first observed humpback whales (*Megaptera novaeangliae*) in Machalilla National Park, Ecuador (Fig. 1) in the late 1980s (Félix and Haase, 2001). These animals are thought to be contiguous with a larger Southern Hemisphere humpback whale stock, and typically spend June to September in the area to calve and mate (Scheidat *et al.*, 2000). A preliminary abundance estimate for this breeding population, based on capture-recapture statistics from an ongoing photo-identification study, is 400 animals (Scheidat *et al.*, 2000). For a number of logistical and other reasons, little information is available on humpback whales from Central and South America.

The tourism industry in Ecuador recognised the economic value of these whales only five years ago. Whalewatching is a particularly lucrative industry in many parts of the world, and is often cited as an economic alternative to whaling (e.g. Hoyt, 1995). However, it has been recognised for many years that harassment by vessels can have both short- and long-term effects on humpback whales (e.g. Norris and Reeves, 1978). Short-term effects have the advantage of being easily demonstrated in terms of avoidance and aggressive behaviours, although whether long-term effects occur is more significant at the population level. Absence of proper controls makes it more difficult to create causal linkages between long-term human activity and changes in abundance and distribution of animals.

Repeated disturbance of critical behaviours such as feeding, resting and mating can reduce the biological fitness of the population. While on the mating and calving grounds,

humpback whales rely on blubber reserves obtained during the feeding season, and therefore may be exceedingly vulnerable to energetic costs of repeated disturbance. Young calves are especially dependent on sufficient time with their mothers to suckle and rest. For them, any disruption carries energetic costs. Studies that quantify the nature and extent of short-term behavioural responses to human disturbance can be useful for alerting researchers to potential population-level effects while they are still reversible. Monitoring the extent of disturbance in breeding areas is especially important.

Despite the relatively recent commercialisation of whalewatching off Ecuador, interest in humpback whales as a tourist attraction has increased dramatically. The waters around Isla de la Plata are becoming known as a good destination for seeing humpback whales, although tourist activity in the waters around Isla de la Plata is not restricted to whalewatching alone. Vessels generally leave Puerto Lopez (Fig. 1) between 0800 and 1000 and arrive in the waters around the island one to two hours later. Tourists may spend several hours on the island and most vessels leave again between 1400 and 1600 to return to the mainland. Vessels typically stop to observe opportunistically whenever sightings of humpback whales are made, rather than searching for whales.

Park managers and conservationists are now concerned that any harassment of whales by whalewatchers could disrupt their reproductive and social activities and, ultimately, displace the animals from the area. However, all realise that whalewatching has become an important part of the local economy. The need to protect the humpback whales

* FTZ Westküste Büsum, Hafentörn, 25761 Büsum, Germany.

⁺ Casilla 17-21-872, Quito, Ecuador.

[#] Sea Mammal Research Unit, Gatty Marine Laboratory, St Andrews, Fife KY16 8LB, Scotland.

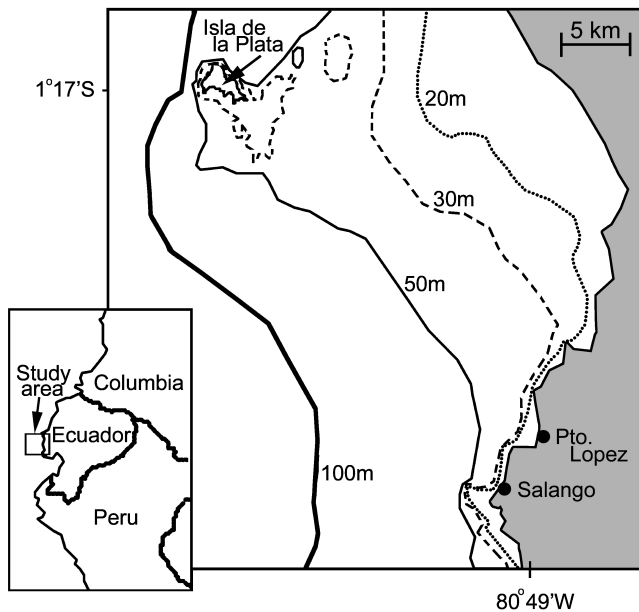


Fig. 1. Map of study area

has become a necessity, not only from the whales' perspective, but also to provide an alternative and potentially sustainable income to a coastal community in a developing country.

It is difficult to determine reactions of cetaceans towards vessels. For example, if using a vessel then the observation platform may also be influencing the effect to be measured. In a few locations, land-based studies are possible. This approach provides an independent platform that has no influence on the whales' behaviour. It also allows the use of theodolites to measure speed or features of the whale's path in the absence of boat traffic (Würsig *et al.*, 1991).

Isla de la Plata was used as such a platform to begin to examine whether the activity of local whalewatching vessels is altering certain aspects of the behaviour of humpback whales. A brief pilot study in 1997 located a cliff on the eastern point of Isla de la Plata as a reliable place from which to observe whales and whalewatching vessels. From here, groups of whales were observed before and/or after encounters with whalewatching boats. The study was designed to measure certain short-term reactions of humpback whales to typical vessel activity in this area. The two aims were: (1) to identify the nature of any avoidance response in order to draft whalewatching guidelines to help local mariners identify when they may be disturbing whales; and (2) to quantify the magnitude of any avoidance response, to see how this relatively understudied population behaves around boats compared with whales in other whalewatching areas.

METHODS

The behaviour of humpback whales and the activity of whalewatching boats were observed from Isla de la Plata between 7 July and 28 August 1998, and between 27 July and 27 September 1999. The 90m height of the observation point, Escalera, allowed long-range observation of several groups, and enabled the team to monitor groups long enough to obtain pre-, during- and post-exposure observations. The height of the observation point was obtained using a detailed contour map of the island provided by Fundación Natura,

Ecuador. The focal plane of the theodolite was established as 91.5m above mean sea level (including the height of the theodolite and tripod).

As whales or groups of whales entered the study area, the centroid of the group was tracked using a WILD theodolite (with automatic vertical index) mounted on a tripod, using the methods described in Würsig *et al.* (1991). An example of a typical tracking is shown in Fig. 2. Whales were tracked from the moment they entered to the moment they exited the field of view. A group of whales was defined as animals that were swimming within three body lengths of one another. Vertical and horizontal angles at each theodolite reading were measured to the nearest 20 seconds of arc. Time was recorded to the nearest second. Group activity, group size and group composition (number of calves present) were noted at the beginning and end of each observation session and if these parameters changed. The horizontal distance from the observation point at sea level to the whales was calculated using the trigonometric relationships between the vertical and horizontal angles of sightings and the known height of the theodolite (Davis *et al.*, 1981). Approximate fixes (for example, those made on the 'footprint' left by the whale) were omitted from all calculations. Changes in height of the water level were ignored, but are negligible (< 1%) due to the height of the cliff and the small tidal movements in the study area. In many studies, this is key, since percent errors in cliff height and swim speed tend to be approximately equal (Würsig *et al.*, 1991).

Two candidate response variables were calculated. The mean swim speed of the group was averaged across a tracking session using the distance between two points and the time taken to cover this distance. The directness index of a group of whales was calculated dividing the 'crow's flight' distance (between the first and the last position of a tracking session) by the cumulative surface distance covered between all recorded positions (Fig. 3). This index is equivalent to the milling index of Tyack (1982). Its value ranges from 1 (when animals move in a straight line) to 0 (when animals swim in a circle, that is, end up in the starting position).

Tracking sessions were targeted when humpbacks entered the study area unaccompanied by whalewatching boats. When a boat or boats approached focal animals, the position of each boat was recorded at least twice during a theodolite tracking session. The maximum number of boats ever observed near whales was nine (Scheidat, unpublished data). However, during the natural experiments, the number of boats accompanying the whales was either one or two. The whales continued to be tracked when associated boats left the focal animals, in order to obtain a sample of whale behaviour under pre-, during, and post-exposure conditions. Subsequent analyses were restricted to interactions when observation time with and without vessels were each 20 minutes long, and when at least five whale positions were recorded under each traffic condition.

RESULTS

Tracking humpbacks and whalewatching vessels

In 1998 and 1999, a total of 73 opportunistic observations were made under a variety of traffic conditions. On 27 of those occasions, natural experiments occurred that enabled comparison of pre- to during-exposure ($n = 12$) or during- to post-exposure ($n = 15$) behaviour. These pairing categories are mutually exclusive, such that a during-vessel behavioural observation is compared with either pre-vessel or post-vessel behaviour, but not both. Consequently, the pre- to during-treatment samples are statistically independent from

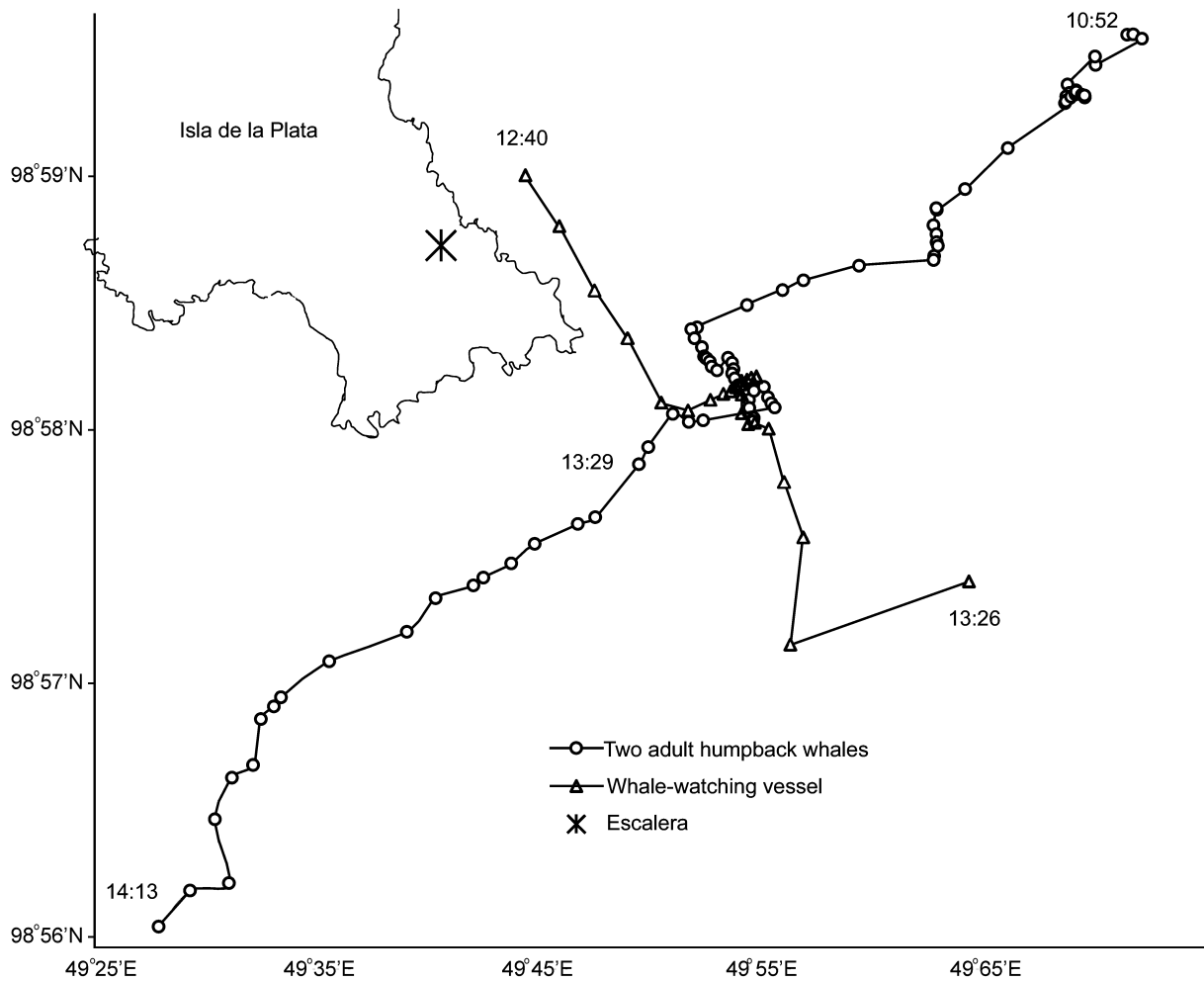


Fig. 2. Example of a typical theodolite tracking from the Isla de la Plata. The observations were made from the observation point Escalera at a focal height of 91.5m. The tracking took place on the 25 August 1999. A group of two adult whales was first noted at 10:52 moving slowly in a southwesterly direction. They were joined by a whalewatching vessel at 12:54 that stayed with the group until 13:18. The humpbacks showed milling and resting behaviour until about 13:28 when they started to travel. The map is presented using a UTM (Universal Transverse Mercator) projection for zone 17 (78°W to 84°W). The x-Axis represents the distance in metres from the central meridian of zone 17 (81°W) and the y-Axis represents the distance in metres from the South Pole.

the during- to post-treatment samples: each group of whales serves as its own control, and a day's tracking session of a group yields only one pair of observations.

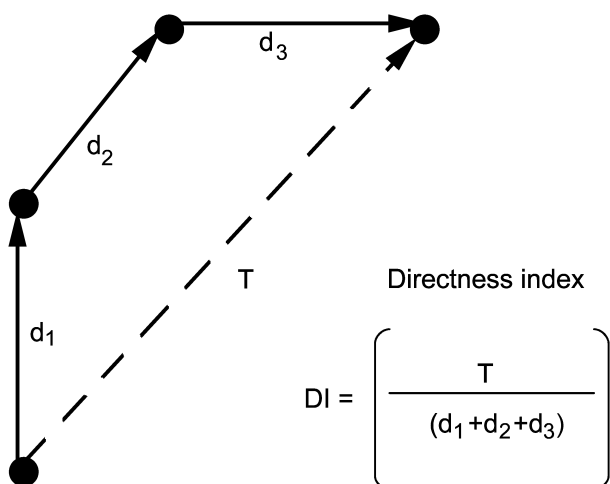


Fig. 3. A sample swimming path with four surfacings (●) and three dives (d_i), showing a measure of path predictability called the directness index. The directness index is the ratio of the track diameter (T) to its perimeter.

Pre-, during, and post-treatment observations were each 20 minutes long with at least five theodolite positions recorded. The remaining, opportunistic observations varied widely in terms of track length and number of positions recorded. Consequently, the analyses presented here are restricted to those observations of natural experiments, where local whalewatching traffic conditions form the treatment.

Changes in swim speed and path directness

Histograms of speed and directness index revealed some evidence of positive skew. Rather than performing Kolmogorov-Smirnov tests, which often fail to detect true deviations from the normal distribution in small samples (Zar, 1998), non-parametric tests were performed. The Wilcoxon matched-pairs test (the non-parametric equivalent of the paired t-test) was chosen as the most conservative way to analyse these data while retaining sufficient power to detect a true effect (Stewart-Oaten, 1995).

On 12 occasions, whale behaviour was recorded in the absence of vessel traffic and during subsequent exposure to either one ($n=6$) or two ($n=6$) whalewatching boats. In these cases, mean speed of humpback whale groups increased significantly from 2.97km h^{-1} to 4.52km h^{-1}

during the vessel interaction (Wilcoxon test for paired data; $Z=2.04$, $p=0.041$; Fig. 4). No significant change in directness index was observed ($Z=0.94$, $p=0.346$; Fig. 4).

On 15 additional occasions, humpback whales entered the study area already accompanied by one ($n=11$) or two ($n=4$) whalewatching vessels. In these cases, whale behaviour was recorded in the presence of the whalewatching traffic as well as after the vessel(s) left. Whale behaviour was compared during the 20 minutes immediately before the boat left, to the first 20 minutes of behaviour recorded post-treatment. Speed did not decline significantly after the vessel left (Wilcoxon-test for paired data; $Z=1.70$, $p=0.088$). Whales' paths, however, became significantly more direct (from a mean directness index of 0.59 during interactions to a mean of 0.76 after the whalewatching boat left, $Z=2.22$, $p=0.027$; Fig. 4).

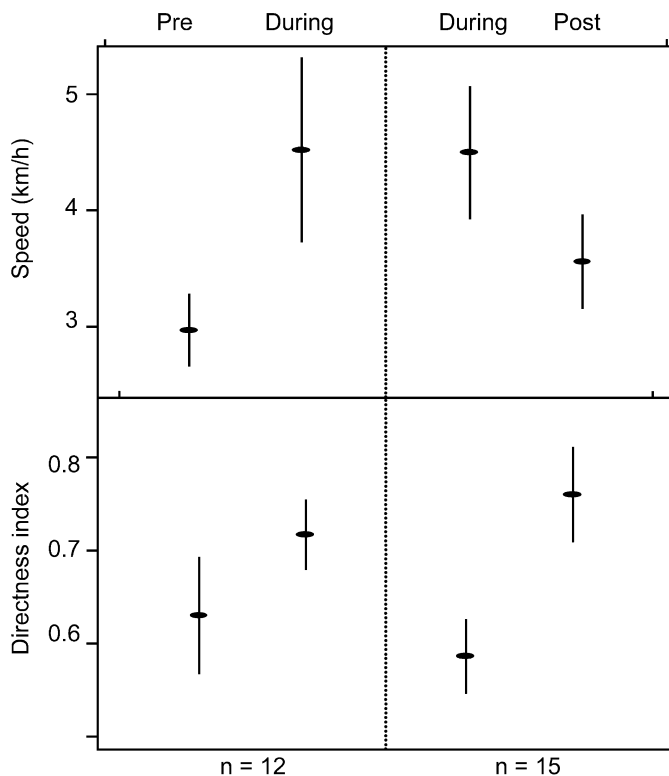


Fig. 4. Behavioural responses (mean \pm SE) of humpback whales after the approach (left) or departure (right) of whale-watching traffic.

DISCUSSION

The study successfully addressed the goal of identifying the nature and magnitude of certain short-term behavioural responses of humpback whales to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador. The data show that these humpback whales increased swim speed when approached by local whalewatching boats. Au and Green (2001) and Bauer *et al.* (1986) have reported that Hawaiian humpbacks also responded to the presence of boats with a stereotyped response of increasing swim speed. Weak evidence ($p=0.088$) was found that swim speed decreased in the 20mins of observation after boats left. Whilst this is not significant at the $p=0.05$ level, it is suggestive of the prediction that the effect is short lived. However, additional experiments are required to confirm or deny this.

Similarly, while our results show that the whales adopted a more predictable path after the boats left, this may not be evidence of immediate recovery after short-term disturbance

but may reflect a statistical artefact of our [namely, visual] versus the whale's [ostensibly acoustic] perception of the node dividing no-boat from boat traffic conditions. Without a causal linkage between decreasing path directness and boats approaching, it is difficult to account for the adoption of a straighter path after the boat leaves. Further experiments are required that *inter alia* record the position of a greater number of surfacings, to demonstrate a convincing causal relationship between the presence of vessels and the directness of whales' paths.

A further limitation of the present study is that it was limited to cases with only one or two vessels approaching the focal group. A similar study on killer whales in Canada, suggested that whales may perceive one boat differently than many (Williams *et al.*, 2002). In reality many boats may arrive at the same time in our study area. Further experiments are required to test the effects of a large number of boats 'crowding' whales.

Clearly, cetaceans display a wide range of reactions to human activity. For example, they may approach a vessel, move away from a vessel or apparently not react at all. Cetacean reactions will not all be visible to a human observer, as changes in behaviour or swimming speed are; nor are they necessarily problematic in their own right. However, long before whales show responses that are obvious at the surface, they are likely to react at a physiological level. Despite this, for practical reasons, when investigating reactions of whales to humans, as in the present study, we usually rely on behaviour that is noticeable and measurable, treating this an indicator of potentially important physiological changes.

Reactions of humpback whales to various types of vessels vary considerably among populations, locations and time of year. Watkins *et al.* (1981) reported that passage of a tanker within 800m did not disrupt feeding animals; humpback whales generally seem less likely to react when actively feeding compared to resting or when engaged in other activities (Krieger and Wing, 1984; Krieger and Wing, 1986). In contrast, in a study of the effects of vessel noise on humpback whales summering in Alaska, Baker and Herman (1989) demonstrated a number of significant responses including increases in dive durations and orientation away from the path of moving boats, often at ranges of up to 3-4km.

Bauer (1986) and Bauer and Herman (1986) reported short-term reactions of breeding humpback whales to vessels in Hawaiian waters. Results differed among age-sex class, depending whether the sighting consisted of singers, other lone animals, mothers or calves. In general, Hawaiian humpback whales attempted to avoid vessels by making longer dives, swimming away from the path of the vessel, and sometimes by demonstrating agonistic behaviours. Some agonistic behaviours were observed in the current study, such as charging or tail slapping, between whales as well as towards vessels. These results are not presented however because it is difficult to ascertain whether rates of surface-active behaviour were collected in an unbiased way (for example that independent events were assigned to a given individual, that bouts of surface activity were recorded as a single event, and/or that events recorded under high-traffic conditions were as likely as when whales were unaccompanied by boats).

Some data on long-term changes in behaviour or habitat-use by humpback whales appear contradictory. On the summer feeding grounds off Cape Cod, humpback whales remain for extended periods and return annually despite exposure to many ships, fishing vessels and

whalewatching boats (e.g. Beach and Weinrich, 1989; Clapham *et al.*, 1993). However, there is some indication that humpback whales do change habitat use in response to human disturbance. For example, Herman (1979) suggested that humpback whale density may be inversely related to the daily amount of boat traffic and to the local amount of human activity in Hawaii.

Despite this, there is evidence that the Hawaiian population is increasing, suggesting that any long-term negative effects are not apparent at the level of the population (Bauer *et al.*, 1993).

The annual return of humpback whales to feeding and breeding grounds *per se* is unconvincing evidence that whalewatching traffic is not disruptive, since strong residency patterns can be found with both weak and strong levels of disturbance; even highly localised whaling activities often failed to disrupt conservative migratory traditions (e.g. Chittleborough, 1965). While strong site fidelity may be interpreted as evidence that animals are fairly tolerant of human disturbance and will probably not change their habitat due to vessel presence, it may equally indicate the extreme importance of some areas to the biology of the whales.

One of the challenges in studying behaviour is to take into account individual variation when arriving at general conclusions. The present study attempted to address this by targeting observations of a wide range of subjects: lone animals, mother-calf pairs and groups of up to six adults. To the best of our knowledge, no group is represented more than once in the analyses. Ideally, photo-identification studies should be undertaken to allow focal animals to be identified. Unfortunately, limited resources prevented this. However, we recognise the need for this to occur in future studies, although care must be taken to ensure that any disturbance associated with taking photographs does not confound the results. Knowledge of individuals also allows more targeted experiments to be carried out. Combined studies can have both practical and cost benefits, the latter being particularly important in a developing country. Finally, experimental approaches to a variety of individuals and groups are required to confirm whether the 85 whales observed in this study behaved in a way that typifies the population of approximately 400 animals.

The fact that Machalilla humpback whales respond to the arrival of whalewatching vessels by increasing their swim speed is cause for concern. As expected for whales on their breeding grounds, no feeding has been observed. Consequently they must rely on fat reserves to meet their high energetic demands – the females to calve and lactate, and the males to engage in active reproductive displays. Some long-term Hawaiian studies suggest that mother-calf pairs become proportionally less frequent close to shore when recreational boating increases (Glockner-Ferrari and Ferrari, 1985; 1990; Salden, 1988). Mother-calf pairs may be especially vulnerable to disturbance, since some potential avoidance responses (of increased swim speeds and longer dive times, for example) may be beyond the physiological limits of the calf, and because calves may have less opportunity to suckle if the mother is forced to increase her speed or to change her behaviour from resting to travelling.

Williams *et al.* (2002) measured behavioural responses of northern resident killer whales to an experimental whalewatching boat, and found that animals generally evaded the boat by adopting a more circuitous path. This evasive response, when compared with a wider range of opportunistic observations, tended to increase in magnitude

as boats got closer. The results from the current study, however, suggest that humpback whales respond to whalewatching boats with a stereotyped tendency to increase swim speed (c.f. Bauer, 1986; Au and Green, 2001).

Of course, fasting puts breeding humpback whales in a qualitatively different context than foraging killer whales. It is unwise to equate swimming faster with a costlier behavioural response than swimming further to get where one wants to go. Neither is it appropriate to speculate whether fasting animals (which vary widely in the thickness of their blubber layers) are less able to cope with repeated short-term disturbances than foraging animals (which may vary widely in their foraging efficiency and prey availability). However, the nature and apparent strength of humpbacks' response to disturbance is striking. It is noteworthy that a variety of studies have detected increased swim speeds as a stereotypical response of baleen whales to vessel traffic (Bauer, 1986; Corkeron, 1995; Au and Green, 2001), given the unlikelihood that that this response can be successful in mitigating disturbance from motorboats. Similarly, it is interesting to note that humpback whales increased speed by over 50% (Fig. 2) in this study, and perhaps as much as 300% in Hawaii (Au and Green, 2001), while the mean response of male northern resident killer whales to a single whalewatching boat was to adopt a path that was 13% less direct (Williams *et al.*, 2002).

Ultimately, studies of whale behaviour around boats are limited by their ability to estimate the extent to which short-term behavioural changes affect the fitness of individuals. Continuing monitoring on the level of the individual is critical to detect any long-term effects of human disturbance. Photo-identification data from this study show that some individual humpback whales are sighted repeatedly throughout a season, as well as between years (Scheidat *et al.*, 2000). On the one hand, this means that individuals are potentially exposed to repeated disturbance, not only on a single day but for up to several months during one year. The area around Isla de la Plata seems to form critical habitat for humpback whales. This makes it both especially important to whales as well as an area where whales are likely to be exposed to disturbance. Between-year site fidelity of some animals may allow for repeated disturbance, and potentially habituation. On the other hand, the wide range of group composition observed during this two-year study suggests that it is unlikely that the observed sample is pseudo-replicated. Further photo-identification studies along the Ecuadorian coast, as well as comparisons with unpublished datasets from other nearby breeding grounds are needed. Should those efforts succeed, it will then be possible to look at vessel impacts at the level of individuals. It is hoped that the findings from this study provide a useful starting point to estimate the cost of this relatively new vessel traffic to some whales in poorly studied waters.

Mobley *et al.* (1999) found that whalewatching is not having an effect on the apparently slow recovery of the Hawaiian humpback whale population. Before reaching similar conclusions for humpback whales in Ecuador, longer-term monitoring and a concerted, collaborative effort to test a wider variety of traffic conditions is required. In the meantime, it seems sensible to manage whalewatching activity in Ecuador as though short-term behavioural responses signify underlying disturbance that may have currently undemonstrated long-term impacts. Experimental studies to determine which whalewatching boats and activities elicit the weakest behavioural responses are strongly recommended. Although local whalewatching

guidelines exist, they are not legally binding, and reflect perceived rather than demonstrated impacts of vessel traffic. In order to produce biologically relevant guidelines, experimental testing of relationships between whale behaviour and vessel type, number and proximity are encouraged. In the meantime, it has been recommended that boats limit their closest approach to 100m, and that no more than two boats be allowed within 1,000m at a time until future experimental studies identify more appropriate guidelines. Similarly, local whalewatch operators have been made aware that if they have to speed up their boats to keep up with whales, then this may be a sign that the whales are disturbed. Cooperation between environmental agencies and local stakeholders is especially critical for managing whalewatching in this developing country, where sustainability of the whalewatching industry may be a bigger concern among decision-makers than the well being of the whales.

ACKNOWLEDGEMENTS

This study was financed with grants from the German Academic Exchange Program (DAAD), the Jane Marcher Foundation, as well as yaqu pacha e.V. (Organisation for the Conservation of Aquatic Mammals in South America). We would like to thank the volunteers who worked under often difficult conditions on the island. We would like to thank also the Machalilla National Park for permission to work from the island, and local whalewatching operators for logistical support throughout this study.

REFERENCES

- Au, W.W.L. and Green, M. 2001. Acoustic interaction of humpback whales and whalewatching boats. *Mar. Environ. Res.* 49:469-81.
- Baker, C.S. and Herman, L.M. 1989. Behavioural responses of summering humpback whales to vessel traffic. Experimental and opportunistic observations. NPS-NR-TRS-89-01. Report from Kewalo Basin Marine Mammal Laboratory, Honolulu, for the US National Park Service, Anchorage, AK.
- Bauer, G.B. 1986. The behavior of humpback whales in Hawaii and modifications of behavior induced by human interventions. Ph.D. Thesis, University of Hawaii, Honolulu.
- Bauer, G.B. and Herman, L.M. 1986. Effects of vessel traffic on the behavior of humpback whales in Hawaii. Report from Kewalo Basin Marine Mammal Laboratory, Univ. Hawaii, Honolulu, for the US National Marine Fisheries Service.
- Bauer, G.B., Mobley, J.R. and Herman, L.M. 1993. Responses of wintering humpback whales to vessel traffic. *J. Acoust. Soc. Am.* 94(3, Pt 2):1848.
- Beach, D.W. and Weinrich, M.T. 1989. Watching the whales: is an educational adventure for humans turning out to be another threat for endangered species? *Oceanus* 32(1):84-8.
- Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16(1):33-128.
- Clapham, P.J., Baraff, L.S., Carlson, C.A., Christian, M.A., Mattila, D.K., Mayo, C.A., Murphy, M.A. and Pittman, S. 1993. Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine. *Can. J. Zool.* 71(2):440-3.
- Corkeron, P.J. 1995. Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: Behaviour and responses to whale-watching vessels. *Can. J. Zool.* 73(7):1290-9.
- Davis, R.E., Foote, F.S., Anderson, J. and Mikhail, E. 1981. *Surveying Theory and Practice*. McGraw Hill, New York. 992pp.
- Félix, F. and Haase, B. 2001. The humpback whale off the coast of Ecuador, population parameters and behavior. *Rev. Biol. Mar. Oceanog.* 36(1):61-74.
- Glockner-Ferrari, D.A. and Ferrari, M.J. 1985. Individual identification, behavior, reproduction and distribution of humpback whales, *Megaptera novaeangliae*, in Hawaii. MMC-83/06. Final report to US Marine Mammal Commission, Washington, DC. 35pp. NTIS PB85-200772. [Available from: www.ntis.gov].
- Glockner-Ferrari, D.A. and Ferrari, M.J. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975-1988: the life history, reproductive rates, and behaviour of known individuals identified through surface and underwater photography. *Rep. int. Whal. Commn* (special issue) 12:161-9.
- Herman, L.M. 1979. Humpback whales in Hawaiian waters: a study in historical ecology. *Pac. Sci.* 33(1):1-15.
- Hoyt, E. 1995. The worldwide value and extent of whale watching 1995. A special report from the Whale and Dolphin Conservation Society. 36pp. [Available from: sarahcl@wdfs.org.uk].
- Krieger, K.J. and Wing, B.L. 1984. Hydroacoustic surveys and identification of humpback whale forage in Glacier Bay, Stephens Passage, and Frederick Sound, southeastern Alaska, summer 1983. NOAA Tech. Memo. NMFS F/NWC-66. U.S. Natl. Mar. Fish. Serv., Auke Bay, AK. NTIS PB85-183887. [Available from: www.ntis.gov].
- Krieger, K.J. and Wing, B.L. 1986. Hydroacoustic monitoring of prey to determine humpback whale movements. NOAA Tech. Memo. NMFS F/NWC-98. U.S. Natl. Mar. Fish. Serv., Auke Bay, AK. 62pp. NTIS PB86-204054. [Available from: www.ntis.gov].
- Mobley, J., JR, Bauer, G.B. and Herman, L.M. 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Aquat. Mamm.* 25(2):63-72.
- Norris, K.S. and Reeves, R. 1978. Report on a workshop on problems relating to humpback whales (*Megaptera novaeangliae*) in Hawaii. Report to US Marine Mammal Commission, Washington, DC.
- Salden, D.R. 1988. Humpback whale encounter rates offshore of Maui, Hawaii. *J. Wildl. Manage.* 52(2):301-4.
- Scheidat, M., Castro, C., Denking, J., González, J. and Adelung, D. 2000. A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador. *J. Cetacean Res. Manage.* 2(3):165-72.
- Stewart-Oaten, A. 1995. Rules and judgements in statistics: three examples. *Ecology* 76:2001-9.
- Tyack, P. 1982. Humpback whales respond to sounds of their neighbors. Ph.D. Thesis, Rockefeller University, New York. 198pp.
- Watkins, W.A., Moore, K.E., Wartzok, D. and Johnson, J.D. 1981. Radio tracking of finback *Balaenoptera physalus* and humpback *Megaptera novaeangliae* whales in Prince William Sound, Alaska. *Deep-Sea Res.* 28A(6):577-88.
- Williams, R., Trites, A.W. and Bain, D.E. 2002. Behavioural responses of killer whales to whale-watching traffic: opportunistic observations and experimental approaches. *J. Zool., London.* 256:255-70.
- Würsig, B., Cipriano, F. and Würsig, M. 1991. Dolphin movement patterns: information from radio and theodolite tracking studies. pp. 79-111. In: K. Pryor and K.S. Norris (eds.) *Dolphin Societies, Discoveries and Puzzles*. University of California Press, Berkeley, California, USA. 397pp.
- Zar, J.H. 1998. *Biostatistical Analyses*. Prentice Hall, New Jersey, USA. 929pp.