Risso's dolphin alters daily resting pattern in response to whale watching at the Azores

Fleur Visser[1,2], Karin L. Hartman[2], Ente J.J. Rood[1,2], Arthur J.E. Hendriks[2], Daan B. Zult[3], Wim J. Wolff[4], Jef Huisman[1] and Graham J. Pierce[5,6]

[1]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam
Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands

[2]Nova Atlantis Foundation
Rua dr. A. Freitas Pimentel 11, 9930-309, Santa Cruz das Ribeiras, Pico, Azores, Portugal

[3]Department of Psychology, University of Amsterdam. Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands

[4] Department of Marine Benthic Ecology and Evolution, Groningen University
P.O. Box 14, 9750 AA Haren, The Netherlands

[5]Oceanlab, University of Aberdeen
Main Street, Newburgh, Aberdeenshire, AB41 6AA, UK

[6]Instituto Español de Oceanografía, Centro Oceanográfico de Vigo
P.O. Box 1552, 36200, Vigo, Spain

Corresponding author:
Fleur Visser, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam.
Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands
Email: F.Visser@uva.nl

Abstract

Behavioral responses of Risso’s dolphins (*Grampus griseus*) to whale-watching vessels were studied off Pico Island, Azores. Dolphin behavior was studied from land, enabling observations of groups in the absence and presence of vessels. The number of whale-watching vessels showed a clear seasonal pattern, dividing the whale-watching period in a low season and a high season. During the low season, Risso’s dolphins rested mainly in the morning and afternoon. During the high season, this bimodal pattern changed markedly and Risso’s dolphins rested mainly at noon, when the number of active vessels was lowest. Also, significantly less resting was observed during the high season. Data analysis using a generalized additive model (GAM) showed that this change in resting behavior was strongly associated with vessel abundance and pointed to a threshold vessel abundance. When more than four vessels were present, Risso’s dolphins responded by shifting from resting to traveling behavior. During the high season, this threshold vessel abundance was exceeded during 19% of observation days. Reduced resting rates can have negative impacts on the build-up of energy reserves and ultimately on reproductive success. We suggest management measures regulating the timing and intensity of whale-watching activities.

Deleted: We had the exceptional opportunity to study

Deleted: d

Deleted: in the

Deleted: to

Deleted: e. The analysis

Deleted: ,

Keywords:

Risso’s dolphin, *Grampus griseus,* whale watching, Azores, behavioral budget, land observations, resting behavior

Introduction

Whale-watching tourism has grown to a great extent over the last few decades, leading to a strong rise in the exposure of cetaceans to boat traffic and interactions with humans (Miller 1993, Hoyt 2001 use revised IFAW 2009 report). Although marine ecotourism can benefit the conservation of cetacean species through the increase of public awareness (Duffus and Dearden 1990), whale-watching activities also may have harmful effects on the animals. Cetaceans have shown a range of short- to long-term behavioral reactions to whale-watch vessels; several that seem comparable to predator-avoidance responses (*e.g.* Williams *et al.* 2002). These responses include horizontal and vertical avoidance (Janik and Thompson 1996, Nowacek *et al.* 2001, Williams *et al.* 2002), change in vocalizations (Richardson *et al.* 1995), changes in activity and energy budgets (Lusseau 2003*a*, *b*, 2004; Williams *et al.* 2006), changes in habitat use (Baker and Herman 1989, Allen and Read 2000), displacement (Kruse 1991, Lusseau 2005), and a decline in abundance in small, resident populations (Bejder *et al.* 2006).

Deleted: also
Deleted: In response to whale-watching vessels, c
Deleted: term
Deleted: ,
Deleted: of which
Deleted: in some cases even
Deleted: of
Deleted: population

The nature and strength of cetacean responses to whale watching has been linked to the intensity of vessel traffic, human swimming activities, and vessel conduct (Bejder *et al.* 2006, Stensland and Berggren 2007, Williams and Ashe 2007). The response also depends on cetacean behavior prior to exposure, the age and sex of individuals, their past experiences and habituation (*e.g.* Erbe 2002). Cetaceans may react to vessel noise because it interferes with their capacity for communication, hearing and orientation (Van Parijs and Corkeron 2001, Erbe 2002) and they also may try to avoid vessels to reduce the risk of injury (Constantine 2001, Constantine *et al.* 2004;

Deleted: ,
Deleted: also

Lusseau 2003b). Nevertheless, it can be difficult to relate any observed short-term response to vessel (vessels in general?) presence to long-term biological effects on cetacean populations. However, changes in behavior often are related to the energy budget of individuals, and therefore can provide information on the biological significance of an impact at the population level (Bejder and Samuels 2003). A decrease in resting behavior of cetaceans in response to human disturbance has frequently been observed and directly affects their energy budget (*e.g.* Constantine 2001, Lusseau 2003*a*). I believe these are examples of resident populations- some small and with habitat partitioning)

Deleted: often

Deleted: thereby

Deleted: ,

Whale-watching tourism in the Azores has been growing rapidly since its start in 1992, following an era of whaling on the sperm whale (*Physeter macrocephalus*). High cetacean diversity has made whale watching one of the most important tourist attractions of the archipelago (Magalhães *et al.* 2002, MARE 2002). In 2004, fifteen tour operators offered daily trips from seven islands of the Azores, the islands of Pico and Faial being the main centres of activity. Local legislation to regulate whale-watching activities was implemented in 1999, including guidelines on approach distances, duration of interactions, angle of approach and maximum number of vessels allowed per cetacean group. Also, more strict regulations apply to groups with calves (Carlson 2008). Swimming is allowed with five species of wild dolphins, including Risso's dolphin (*Grampus griseus*) and bottlenose dolphin (*Tursiops truncatus*). However, compliance with these regulations has been incomplete (qualify incomplete if possible) (Magalhães *et al.* 2002). Due to the presence of cetaceans in inshore waters, whale-watching vessels can be guided very efficiently by an observer

Deleted: the

from land, making it difficult for targeted cetaceans to avoid vessel encounters (this also makes them a potential target of recreational vessels).

Deleted: which makes

Risso's dolphin is one of the target species of whale-watching activities in the Azores (Gomes Pereira 2008). They are relatively shy cetaceans and do not approach boats readily (Tinker 1988). Off Pico Island, more than 1000 individuals have been identified, many of which are present in the inshore waters on a regular basis. Risso's dolphin individuals show high site fidelity in the area, as well as a complex social organization involving stable, long-term bonds and age- and sex-specific social segregation (Hartman *et al.* 2008). Also, a considerable part of the identified population is composed of mother-calf pairs, indicating that the area may serve as a nursing ground. This population structure makes Risso's dolphins in the Azores potentially vulnerable to disturbance.

Deleted: (*Grampus griseus*)

Deleted: the

Deleted: Risso's dolphins

Deleted: readily

To determine the impact of whale-watching activities (on Risso's dolphins) around the Azores, we investigated the effects of vessel presence and abundance on the behavior of Risso's dolphins. Since Risso's dolphins can be observed readily in Azorean inshore waters, we studied the behavior of Risso's dolphins from a land-based platform. Land-based observations have little or no impact on the animals studied, enabling unbiased comparisons of behavior in the absence and presence of whale-watching vessels (Williams *et al.* 2006).

Deleted: in this paper

Deleted: e readily

Deleted: had the unique opportunity to

Deleted: y

Deleted: the advantage that observers have

Deleted: an

Methods

Research area

From May 1 until October 28, 2004, daily land-based observations were made from a fixed look-out at 30 m above sea level on the south coast of Pico island, Azores (38°24’ N, 28°11’ W). The observations were conducted using Steiner Observer binoculars (Steiner Binoculars, Bayreuth, Germany), with 25x magnification and 80 mm objective lenses. The sighting range from our land-based look-out was determined empirically by recording the GPS locations of our research vessel at the limits of the sighting range. Results indicate that the sighting range from the look-out was 11 nautical miles (Nm) offshore, encompassing a research area of 115 Nm^2 (Fig. 1) and that the presence of Risso’s dolphin could be determined reliably up to 8 Nm offshore. Whale-watching companies operating in the research area generally organize two trips per day. Trips usually last 3-4 hours, starting at 09:30/10:00 h and at 14:00/14:30 h, with occasional evening or whole day trips. Most vessels observed in the research area depart from the harbor of Lajes do Pico (Pico Island); the remainder depart from Madalena (Pico Island), or Horta (Faial Island).

Deleted: shore

Deleted: This showed

Deleted: .

Deleted: presence

Deleted: occasionally extended

Deleted: an

Deleted: trip

Data collection

Observations were conducted daily, at regular intervals between sunrise and dawn. Two types of sampling were used: surveys and focal follows. Sea state on the Beaufort scale (Bft), visibility and weather conditions were recorded at the start of each observation and whenever a change in these variables was observed. Standardized surveys, conducted at the start of all observations, consisted of a scan of the research area, recording the number of Risso’s dolphin groups and individuals and the number of whale-watching vessels present (point sampling; Mann 1999). The area was scanned twice to account for individuals submerged or missed during the

Deleted: ,

first scan. Surveys had a duration of 15-30 minutes to allow for comparison between surveys and were spaced at least two hours apart to obtain independent samples.

Behavioral observations recorded during focal follows consisted of sampling of group size, group composition, location, direction and speed of travel, group formation (spacing), display events and behavior of Risso's dolphin groups, using a standardized ethogram (Mann 1999). Behavioral parameters were recorded once every minute. The relatively small average group size of Risso's dolphin largely rules out the vulnerability to sampling bias of focal group sampling (Bejder and Samuels 2003, Hartman *et al.* 2008). Focal groups were followed for at least 15 minutes, unless the group moved too far offshore for reliable observation or sighting conditions deteriorated. We recorded the number of whale-watching vessels present at the start of each observation, and the timing of vessels entering and leaving the research area during the observations.

Behavior of Risso's dolphin

A group of Risso's dolphins was defined as a set of individuals which interacted socially and/or showed coordinated activity in their behavior (Whitehead 2003). In general, Risso's dolphins in the area formed tight groups with interanimal distances <15 m (Hartman *et al.* 2008). The largest group spacings, up to 50 m, were usually observed during foraging. We distinguished four mutually exclusive behavioral types: resting, traveling, socializing and foraging (Altmann 1974, Shane 1990). Resting was defined as individuals organized in cohesive group formation, moving at low speed, with events of logging (define) individuals and characterized by calm, regular surface behavior. Traveling was defined as individuals moving steadily in a directional path, at normal to high speed. Socializing behavior was defined as individuals showing interanimal interaction (contact) and regular surface display events in cohesive group formation, with larger socializing groups generally organized in dynamically interacting sub-groups. Foraging behavior was defined as loosely spaced individuals or pairs, with individuals displaying regular, long, non-synchronized dives.

The behavioral budget and group size of Risso's dolphin were determined from focal follow data. Activity rates were calculated on hourly and monthly time scales from the cumulative time over which a behavioral state was observed divided by the total effort of focal follow observations during that period. Relative abundance of Risso's dolphins was calculated as the average number of individuals present per survey. Observations at Bft >3 or at limited visibility and focal follows <15 minutes were excluded from analysis.

Intensity of whale watching

The intensity of whale watching was determined by calculating vessel abundance on hourly, daily and monthly time scales. Seasonal patterns were quantified by calculating the total number of vessels frequenting the research area per observation day. Based on seasonal variation in whale-watching intensity, the research period was divided into a high season (July and August) and low season (May, June, September and October). Daily patterns were quantified by calculating average vessel abundance at 1 hour-intervals. Whale-watching intensity was calculated for the total period, including days of rough sea state conditions (Bft>3).

Deleted: in the research area

Statistical analysis

We used generalized additive models (GAMs) to examine the effect of vessel presence in the research area on the behavior of the dolphins. GAMs allow for non-linear relationships between variables by fitting smoothed non-linear functions of continuous explanatory variables without imposing parametric constraints (Hastie and Tibshirani 1990). The optimal degree of flexibility that can be justified by the data is estimated using a maximum likelihood function, while restricting the model to avoid overparametrizing or oversmoothing (Wood 2006). The complexity of the smoothing curve representing a relationship is given by the estimated degrees of freedom (edf), where higher numbers of edf indicate a more complex curve. Data were modeled using the MGCV library in R, version 2.7.0 (Wood 2006, R 2009).

The data input for the GAM analysis consisted of the focal follow observations during which dolphin behavior was recorded as binary variable (behavior present/absent) once per minute. Models were fitted separately for each of the four behavioral types. We expected temporal autocorrelation between the data points, which means that the behavior at time t is related to the behavior at time t-n, where n describes the time-lag (in minutes). To correct for temporal autocorrelation, we added the preceding data points at time lags t = 1, 2,…, n as predictor variables in the GAM analysis. This process approximates the fitting of an autoregressive time-series model to data from each focal follow. Time lags were added sequentially, starting with a time lag of 1 minute, until the time lag n at which the novel predictor variable was no longer significant. We were interested in effects of vessel presence on the behavioral budget. Therefore, vessel abundance was included as explanatory variable in the GAM. Although not strictly a continuous variable, it was entered as a candidate for smoothing [s(x)] by MGCV, allowing for a maximum of 3 edf. In addition, dolphin behavior is likely to vary on different temporal scales, and the behavioral budget of Risso's dolphin may, for example, show daily and seasonal variation irrespective of vessel presence. Therefore, we included the effects of time of day and time of year as categorical variables (factors) in our model. The variable time of day was categorized into 2-hour blocks (8:00-9:59; 10:00-11:59, etc.). Likewise, time of year was grouped into three categories: May-June, July-August, and September-October.

The full R code for each behavioral type was thus: {*Behavior_type ~ s(Vessel abundance, k=4) + [as.factor(time of day: time of year)] + [as.factor(predictor(t-1)] + [as.factor(predictor(t-2)]... + [as.factor(predictor(t-n)]*, *family = binomial(link=logit)*}

We followed a backward selection approach to estimate the optimal model (using $P < 0.05$ as selection criterion). In addition, variables were removed from the model only if this did not substantially increase the Akaike information criterion (AIC) of the model. If the estimated number of edf was near 1 for a smoothing term, and there was no apparent pattern in the residuals, then the smoother function was replaced by a linear term.

For those behaviors which showed a significant relation with vessel abundance, we tested for the level that the effect became significant. This was done by treating 'vessel abundance' as a threshold variable (factor), instead of a smoother variable, which was evaluated from a threshold vessel abundance of 1 to 10 vessels in a series of successive runs of the model.

Deleted: at which

Deleted: vessel abundance

All other statistical tests were performed in SPSS, version 12.0. A significance level of P<0.05 was used for all analyses.

Results

Research effort

During 172 observation days, we conducted 448 focal follow observations and 87 surveys during suitable environmental conditions. The focal follow observations yielded 9197 observation records (of 1 minute each) in total, with 4615 observation records in the low season and 4582 observation records in the high season.

Intensity of whale watching

A total of 487 vessel visits was recorded in the research area, including 460 visits of whale-watching vessels and 27 visits of fishing vessels and pleasure boats. Thus, whale-watching vessels constituted almost 95% of all vessels visiting the research area. Whale-watching vessels were present during 42% of the observation days. The whale-watching season started in spring, with one observation of vessel presence in May and daily activities starting in mid-June. Vessel abundance strongly fluctuated over the research period, showing significant differences between months (Kruskal-Wallis Test, H= 93.1, df=5; P<0.001) (Fig. 2). During the high season months (July and August), we recorded 6.0 ± 4.7 (mean ± SD) vessels per day, while we recorded 1.0 ± 1.8 vessels per day during the low season months (May, June, September, October).

The intensity of whale watching showed a bimodal distribution over the day, resulting from the timing of the whale-watching trips (Fig. 3). During the high season, two peaks of high activity, from 10:00-13:00 h and 14:00-1700 h, were separated by a period of less activity from 13:00-14:00 h. During the low season, activities were centered primarily in the morning hours (10:00-13:00 h). On average, we recorded

1.5 - 3 vessels at the same time (watching the same group of Risso's?) during the high season, and 0.5 - 1.5 vessels during the low season.

Risso's dolphin presence and abundance

The presence of Risso's dolphin in the research area was largely continuous, with records during 90% of the observation days and during 74% of the surveys. On average (mean ± SD), we recorded 2.6 ± 2.5 Risso's dolphin groups per survey (range: 0-14). Mean group size (± SD) was 11.1 ± 7.5 individuals with a median group size of 10 individuals (range: 1-50). Risso's dolphin relative abundance did not show significant changes between months over the study period (Kruskal-Wallis test, H =10.2; df=5; P=0.07).

Behavioral budget

Based on focal follow data, Risso's dolphins spent a substantial portion of their time traveling (0.38), socializing (0.27) and resting (0.25), and less time foraging (0.07) in our research area. They spent more time socializing (χ^2 = 155.8; df=1; P<0.0001) and less time resting (χ^2 = 124.2; df=1; P<0.0001) during the high season than during the low season (Fig. 4).

Deleted: the

Deleted: on

Deleted: behavior

Deleted: on

Deleted: behavior

Activity rates varied during the day (Fig. 5). Foraging behavior was observed mainly during the early morning and the latter half of the afternoon (Fig. 5e, f). A similar but less pronounced pattern was observed for socializing (Fig. 5c,d). The time allocated to traveling remained fairly constant over the day (Fig. 5g,h). There was a clear difference in the timing of resting between the low season and high season (Fig. 5a,b). The low season was characterized by a double-peaked resting pattern, with highest resting rates from 9:00 to 12:00 h and from 14:00 to 16:00 h. During the high season, the morning peak of resting activity was absent, while the main resting period was from 13:00 to 14:00 h (Fig. 5b) when vessel abundance was lowest (Fig. 3).

Statistical analysis

To what extent are the daily and seasonal changes in the behavioral budget of Risso's dolphin related to daily and seasonal patterns in whale-watching activities? (reword and edit down). According to our GAM analysis, temporal autocorrelation of the observations occurred at a time lag of 1 minute for all four behavioral types. For resting, the autocorrelation was also significant at a time lag of 2 minutes. The corresponding corrections for autocorrelation are indicated as the predictor (t-1) and predictor (t-2) variables in Table 1. The GAM analysis revealed a significant negative effect of vessel abundance on resting rate (Table 1), where the effect became stronger at a higher number of vessels (Fig. 6a). The time of day and time of year, by themselves, had little effect on the resting rate of Risso's dolphin. The only intrinsic seasonal pattern detected by the model analysis was less resting at 10:00-11:00 h of July and August (Table 1). As a next step, we investigated at which threshold value the vessel abundance started to have a negative impact on resting rate. This revealed that resting rate was negatively affected by whale-watching activities as soon as more than four vessels were present simultaneously in the area (Table 2), consistent with the shape established by the smoothing curve in Figure 6a. During the high season, this threshold value of more than four vessels was exceeded in 429 observation records (i.e., 9.4% of the observation records) spread over 14 observation days (27.5% of the observation days). During the low season, the threshold vessel abundance of four vessels was rarely exceeded (< 1% of the observation records).

In addition, the GAM analysis showed a significant positive effect of vessel abundance on the time allocated to traveling (Table 1, Fig. 6b). Traveling time was increased significantly when more than three vessels were present in the area (Table 2). No intrinsic seasonal pattern for traveling behavior was detected by the model analysis. The time allocated to foraging and socializing was not affected by vessel abundance, but showed significant daily and seasonal variation. That is, foraging was observed more during the afternoon hours from July to October and less during noon (12:00-13:00 h) in July and August (Table 1). Socializing was observed more during the mornings and late afternoon from May-August.

Overall, the statistical analysis showed that Risso's dolphins: (i) displayed seasonal patterns for foraging and socializing; and (ii) spent less time resting and more time traveling during periods of high vessel abundance.

Deleted: ,
Deleted: on
Deleted: on
Deleted: at

Discussion

Behavioral shifts induced by vessel presence

Our results show a significant effect of whale-watching vessels on the resting behavior of Risso's dolphin. Whale-watching vessels usually went out on two daily trips, one in the morning and one in the afternoon. The number of vessels actively whale watching? in the research area showed a clear seasonal pattern, dividing the whale-watching period in a low and high season. During the low season, Risso's

Deleted: the other
Deleted: season
Deleted: a

dolphin displayed a bimodal resting pattern; their resting rate peaked at around 11:00 h and 15:00 h. During the high season, this bimodal pattern changed into a single peak, with highest resting rates at around 13:00 h. As such, the peak resting activity of Risso's dolphin during the high season was shifted to the hours of lowest whale-watching intensity, at lunch-break.

This was not merely a seasonal behavioral pattern. According to our statistical analysis, resting rate showed a significant negative relation with vessel abundance, which explains the differences in resting rate between the low and high season. Other seasonal effects were limited and not related to the observed shift in resting behavior. Moreover, the analysis revealed that the resting rate did not respond linearly to vessel abundance, but showed a threshold relationship. Significant negative effects of vessel abundance on resting behavior could be detected when more than four vessels were present in the area. Conversely, vessel abundance had a significant positive effect on the time allocated to traveling, starting at a threshold vessel abundance of more than three vessels. Thus, high vessel abundance induced a shift in the behavior of Risso's dolphins, from resting to traveling. The threshold vessel abundance inducing this behavioral shift was exceeded during more than 25% of the observation days in the high season.

Our results are consistent with other studies on the impacts of vessels on cetacean behavior (Lusseau 2003a, 2004; Bejder *et al.* 2006). In particular, threshold responses seem inherent in the reaction of cetaceans to vessel traffic. Killer whales, for instance, reacted to whale-watching activities by choosing a less direct travel path in the presence of 1-3 vessels but a straighter path in the presence of >3 vessels

(Williams and Ashe 2007). Bottlenose dolphins spent more time on traveling following interactions with boats (Lusseau 2003a, 2004; Stensland and Berggren 2007), and avoided areas with intense boat traffic (Lusseau 2005). Moreover, bottlenose dolphins chose a more erratic path, with increased surface behavior when >2 vessels were present (Stensland and Berggren 2007). Studies in Shark Bay, Australia, showed that the regular presence of two whale-watching vessels, opposed to zero or one, resulted in a decline of a small, resident population of bottlenose dolphins using the area with whale-watching activities (Bejder *et al.* 2006). I would list only references here. Also, some of these studies use before, during and after observations.

Deleted: the

Deleted: population

Foraging and socializing

The incidence of foraging and socializing behavior did not show a significant relation to whale-watching vessels, which may indicate that these behavioral types are less sensitive to vessel presence. However, foraging primarily occurred outside the high-intensity hours of whale-watching. Foraging activities were concentrated during the early morning and late afternoon, while very little foraging activity was recorded between 10:00 h and 15:00 h. Low foraging rates observed during daytime might be explained by night-time foraging on deep-sea squid, as has been observed for short-finned pilot whales (*Globicephala macrorynchus*) off California (Shane 1995), both species being primarily teuthophagous. This also may explain the relatively high resting rate of Risso's dolphin observed during day-time (25%), compared to other cetaceans (Moberg 2000, Nowacek and Wells 2001, Constantine *et al.* 2003, Lusseau 2003*a*). Foraging rates were higher during the afternoon hours of late summer and autumn, indicating some degree of natural seasonal variation in the

Deleted: mostly took place

Deleted: The l

Deleted: the

Deleted: might also

timing of foraging. Socializing behavior showed seasonal as well as daily variation. Risso's dolphins spent significantly more time socializing during the high season (July and August) and during the morning and afternoon hours of May to August.

Ecological significance

Risso's dolphins were present almost continuously in the study area.and previous research in the area has shown high site-fidelity of individuals and the presence of newborn calves (Hartman *et al.* 2008). According to the behavioral budget recorded in this study, the dolphins displayed a variety of behaviors with considerable time dedicated to social behavior and resting. These results suggest that the waters off Pico Island function as a resting, foraging and nursing area for the (a?) population of Risso's dolphins (and do so on a daily basis for individuals which are present regularly in the area reword to clarify- is most of the population here on a regular basis or only some individuals?).

Areas used for nursing, resting, foraging and/or socializing form important habitats for cetaceans (Hoyt 2005*a*). We observed an overall reduction in daily resting rates and a shift in the daily resting pattern in response to whale-watching vessels consistent with previous work of Lusseau (2003*b*) and Williams *et al.* (2006) on bottlenose dolphins and killer whales. A reduction in resting rates can result in reduced energy reserves and can negatively affect foraging and reproductive success, an effect which has been found throughout the animal kingdom (*e.g.* Ricklefs *et al.* 1996, Grantner and Taborsky 1998, Frid and Dill 2002, Williams *et al.* 2006). Nursing females and their calves form an especially vulnerable group and disturbances by vessels can suppress the build-up of energy reserves, directly

Deleted: on

Deleted: ,

Deleted: almost continuously

Deleted: , and p

Deleted: he present

Deleted: including

Deleted: i

Deleted: and

Deleted: ,

Deleted: Additionally, the area functions as a foraging ground.

Deleted: . This is

Deleted: ,

Deleted: who showed that resting and socializing behavior of bottlenose dolphins and killer whales are sensitive to boat interactions.

Deleted: ,

Deleted: including fish, birds and marine mammals

Deleted: The n

Deleted: especially

Deleted: ,

Deleted: in which

Deleted: , and thereby

affecting reproductive success (Bejder 2005). (clarify this was in a small resident population)

Management implications

Tourism is growing rapidly in the Azorean islands, including a further increase in whale-watching activities. Although whale-watching pressure at present in the Azores is relatively low compared to other regions (Hoyt 2005*b*; Erbe 2002), our results show that four or five vessels in a relatively small area can have a profound effect on the behavioral pattern of Risso's dolphins. Based on these results, we suggest that management efforts in relation to current and future whale-watching activities in the Azores be directed towards management of the number of vessels (all vessels?- if tourism is increasing it may increase the number of pleasure craft in coastal areas).per area. Low-intensity vessel presence did not have a significant, negative effect on observed behavior, providing a reference from which threshold measures of vessel abundance could be determined (see also Williams and Ashe 2007).

Additionally, it would be beneficial to introduce a time period with no whale-watching activity several hours per day, to create sufficient resting opportunities for the Risso's dolphin population (again, would this consider all vessels?). Other target species in the Azores also may benefit, in particular, the bottlenose dolphin(is this a resident population?) a species that also makes extensive use of the area (Silva 2007) and has shown sensitivity to vessel traffic in other areas (*e.g.* Lusseau 2005, Bejder *et al.* 2006).

Deleted: at a fast pace at the
Deleted: growth of
Deleted: It can be argued that
Deleted: at
Deleted: still
Deleted: ,
Deleted: such as the Canary Islands
Deleted:) or British Columbia (*e.g.*
Deleted: .
Deleted: However, as we have demonstrated,
Deleted: should
Deleted: Moreover
Deleted: recommendable
Deleted: time window without
Deleted: ies
Deleted: during
Deleted: also
Deleted: most notably
Deleted: which also
Deleted: many areas around the world

Acknowledgements

We gratefully thank WWF the Netherlands and Greenpeace Netherlands, the Prins Bernhard Cultuurfonds, the Schure-Beijerinck-Popping Fund, the Dr. Catharina van Tussenbroek Foundation, the Foundation Vrijvrouwe van Renswoude and the ANIMATE project (MEXC-CT-2006-042337) for supporting our work. This paper and its contents would not have been possible without the dedication and hard work of our MSc students and volunteer team members, especially Machiel Oudejans and Else Nuyten. Special thanks go out to Dr. Colin MacLeod, and two anonymous reviewers for their thorough and constructive comments that greatly improved the manuscript. This project was carried out under scientific license nr. 4/CN/2004, issued to Nova Atlantis Foundation by the Azorean Department of the Environment, *Direçcao de Regional do Ambiente*, island of Faial.

References

Allen, M.C. and A.J. Read. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Marine Mammal Science 16:815-824.

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behavior 49:227-267.

Baker, C.S. and L.M. Herman. 1989. Behavioral responses of summering humpback whales to vessel traffic: Experimental and opportunistic observations. U.S. Department of the Interior. National Park Service, technical report: NPS-NR-TRS-89-01. 50 pp.

Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. PhD thesis, Dalhousie University, Halifax.

Bejder, L. and A. Samuels. 2003. Evaluating the effects of nature-based tourism on cetaceans. In: N.M. Gales, M. Hindell and R. Kirkwood, eds. Marine mammals and Humans: Towards a sustainable balance. CSIRO Publishing, Collingwood, Australia.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M Heithaus, J. Watson-Capps, C. Flaherty and M. Krützen. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791-1798.

Carlson, 2008. A review of whale watch guidelines and regulations around the world, version 2008. Available at http://www.iwcoffice.org/conservation/whalewatching.htm#regulations. Accessed October 2008.

Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. Marine Mammal Science 17:689-702.

Constantine, R., D.H. Brunton and C.S. Baker. 2003. Effects of tourism on behavioral ecology of bottlenose dolphins of northeastern New Zealand. DOC Science Internal Series 153. Department of Conservation, Wellington, New Zealand.

Constantine, R., D.H. Brunton and T. Dennis. 2004. Dolphin-watching boats change bottlenose dolphin (*Tursiops truncatus*) behavior. Biological Conservation 117:299-307.

Duffus, D.A. and P. Dearden. 1990. Non-consumptive wildlife-oriented recreation: A conceptual framework. Biological Conservation 53:213-231.

Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. Marine Mammal Science 18:394-418.

Frid, A. and L.M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 11. [online] URL: http://www.consecol.org/vol6/iss1/art11/

Gomes Pereira, J.N.D.S. 2008. Daily species checklist from whale-watching—studying the research potential with an Azorean case study. Journal of the Marine Biological Association of the United Kingdom 88:1283–1288.

Grantner, A. and M. Taborsky. 1998. The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: *Cichlidae*). Journal of Comparative Physiology B 168:427-433.

Hartman, K. L., F. Visser and A.J.E. Hendriks. 2008. Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units. Canadian Journal of Zoology 86:294-306.

Hastie, T.J. and R.J. Tibshirani. 1990. Generalized Additive Models. Boca Raton: Chapman and Hall/CRC Press, Hoyt, E. 2001. Whale watching 2001: worldwide tourism, numbers, expenditures and expanding socioeconomic benefits. International Fund for Animal Welfare, Yarmouth Port, Massachusetts.

Hoyt, E. 2005*a*. Marine protected areas for whales, dolphins and porpoises. Earthscan, London.

Hoyt, E. 2005*b.* Sustainable ecotourism on Atlantic islands, with special reference to whale watching, marine protected areas and sanctuaries for cetaceans. Biology and Environment: Proceedings of the Royal Irish Academy 105B:141-154.

Janik, V.M. and P.M. Thompson. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine Mammal Science 12:597-602.

Kruse, S. 1991. The interactions between boats and killer whales in Johnson strait, B.C. Pages 149-160 in: K.S. Norris and K. Pryor, eds. Dolphin societies discoveries and puzzles. University of California press, Berkeley, California.

Lusseau, D. 2003a. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov Chains to model anthropogenic impacts. Conservation biology 17:1785-1793.

Lusseau, D. 2003b. Male and female bottlenose dolphins *Tursiops spp*. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. Marine Ecology Progress Series 257:267-274.

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecology and Society 9:2.

Lusseau, D. 2005. The residency pattern of bottlenose dolphins (*Tursiops spp.*) in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress Series 295:265-272.

Magalhães, S., R. Prieto, M.A. Silva, J. Gonçalves, M. Afonso-Dias and R.S. Santos. 2002. Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale watching vessels in the Azores. Aquatic Mammals 28:267-274.

Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102-122.

MARE, 2002. Praticas de actuacao da actividade maritimo-turistica. Report of the annual meeting on maritime tourism, Azores. Ambiente. Department of the Environment, Pico, Azores.

Miller, M.L. 1993. The rise of coastal and marine tourism. Ocean & Coastal Management 20:181-199.

Moberg, G.P. 2000. Biological response to stress: implications for animal welfare. CAB International, Cambridge.

Nowacek, S.M., R.S. Wells and A.R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota bay, Florida. Marine Mammal Science 17:673-688.

R. 2009. R freeware for statistical computing. Available at: http://www.r-project.org/. Accessed February 2009.

Richardson, W.J., C.R. Greene, C.I. Malme and D.H. Thompson. 1995. Marine mammals and noise. Academic Press, San Diego, CA.

Ricklefs, R.E., M. Konarzewski and S. Daan. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. American Naturalist 147: 1047-1071.

Shane, S.H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island Florida. Pages 245-265 in: Leatherwood, S. and R.R. Reeves, eds. The bottlenose dolphin. Academic press, New York.

Shane, S.H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. Marine Ecology Progress Series 123:5-11.

Silva, M.A.E. 2007. Population ecology of bottlenose dolphins in the Azores Archipelago. PhD thesis, University of St. Andrews, St. Andrews, UK.

Stensland, E. and P. Berggren. 2007. Behavioral changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Marine Ecology Progress Series 332:225-234.

Tinker, S.W. 1988. Whales of the world. Bess Press Inc., Hawaii.

Van Parijs, S.M. and P.J. Corkeron. 2001. Boat traffic affects the acoustic behavior of Pacific humpback dolphins, *Sousa chinensis*. Journal of the Marine Biological Association of the United Kingdom 81:533-538.

Whitehead, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press, Chicago and London.

Williams, R. and E. Ashe. 2007. Killer whale evasive tactics vary with boat number. Journal of Zoology 272:390-397.

Williams, R., A.W. Trites and D.E. Bain. 2002. Behavioral responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology 256:255-270.

Williams, R., D. Lusseau and P.S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301-311.

Wood, S.N. 2006. Generalized additive models: an introduction with R. Boca Raton: Chapman and Hall/CRC Press.

Table 1. Statistical results from the GAM model, investigating the dependence of the four behavioral types on vessel abundance and temporal variables. In this analysis, vessel abundance was treated as a smoother variable. Only variables showing a significant relationship are given. The GAM model was corrected for temporal autocorrelation in the data, as indicated by the predictor variables at time lag t-*n*.

Behavioral type	Factor	Coefficient	SE	Z-statistic	*P*-value
Socializing	Intercept	-4.84	0.16	-29.43	<0.0001
	May-June:8-9 AM	0.74	0.30	2.51	0.01
	May-June:16-17 PM	1.16	0.54	2.15	0.03
	May-June:18-19 PM	0.96	0.41	2.33	0.02
	July-Aug:8-9 AM	0.68	0.28	2.44	0.01
	July-Aug:10-11 AM	0.74	0.29	2.54	0.01
	July-Aug:16-17 PM	0.98	0.32	3.01	0.003
	Predictor (t-1)	7.91	0.18	44.12	<0.0001
Foraging	Intercept	-6.07	0.25	-23.83	<0.0001
	July-Aug:12-13 PM	-3.15	1.35	-2.33	0.02
	July-Aug:14-15 PM	1.21	0.52	2.33	0.02
	Sep-Oct:16-17 PM	1.74	0.60	2.92	0.004
	Predictor (t-1)	9.09	0.34	26.93	<0.0001
Resting	Intercept	-4.17	0.12	-34.34	<0.0001
	July-Aug:10-11 AM	-0.70	0.32	-2.19	0.03
	Predictor (t-1)	6.72	0.38	17.86	<0.0001
	Predictor (t-2)	0.79	0.38	2.08	0.0498
	Smoother term	edf[1]	est. rank[2]	Chi sq.	P-value
	Vessel abundance	2.58	3	10.84	0.01
Traveling	Intercept	-4.04	0.11	-37.68	<0.0001
	Predictor (t-1)	7.33	0.15	49.36	<0.0001
	Smoother term	edf[1]	est. rank[2]	Chi sq.	P-value
	Vessel abundance	1.86	3	9.72	0.02

[1]*Edf = estimated degrees of freedom*

[2]*Est. rank = estimated rank*

Table 2. Statistical results from the GAM model for the dependence of the four behavioral types on vessel abundance and temporal variables. In this analysis, vessel abundance was treated as a threshold variable (factor). Only variables showing a significant relationship are given. The GAM model was corrected for temporal autocorrelation in the data, as indicated by the predictor variables at time lag t-*n*.

Behavioral type	Factor	Coefficient	SE	Z-statistic	*P*-value
Resting	Intercept	-4.13	0.12	-35.29	<0.0001
	July-Aug:10-11 AM	-0.58	0.31	-1.89	0.06
	Predictor (t-1)	6.73	0.38	17.90	<0.0001
	Predictor (t-2)	0.80	0.38	2.12	0.03
	Threshold vessel abun. >4	-1.11	0.44	-2.53	0.01
Traveling	Intercept	-4.09	0.11	-36.83	<0.0001
	Predictor (t-1)	7.33	0.15	49.40	<0.0001
	Threshold vessel abun. >3	0.56	0.24	2.31	0.02

Figure legends

Figure 1. Location of the Azores in the North Atlantic Ocean (left panel). Location of the lookout in Santa Cruz (SC), and the harbors of Madalena (M), Lajes do Pico (L), and Horta (H) from which the whale-watching vessels depart (right panel). The outline indicates the research area off Pico Island covered by our land-based observations from the lookout in Santa Cruz.

Figure 2. Number of whale-watching vessels per day observed during May-October 2004. Shaded area indicates the low season, while the non-shaded area indicates the high season.

Figure 3. Daily distribution of whale-watching vessels (mean ± SE), during the low season and high season. Data are binned in 1-hour intervals (i.e., 8 = interval 8:00– 8:59 h).

Figure 4. Behavioral budget of Risso's dolphin (mean ± 95% CI), for the low season and high season. Trav = traveling; Soc = socializing; Rest = resting; For = foraging.

Figure 5. Daily patterns of resting, socializing, foraging, and traveling (mean ± 95% CI), during the low season (left panels) and high season (right panels). The behavioral budget is expressed as the average activity rate per 1-hour interval (i.e., 8 = interval 8:00 – 8:59 h).

Figure 6. GAM smoothing curves of: (a) resting behavior as function of vessel abundance (edf = 2.58), and (b) traveling behavior as function of vessel abundance (edf = 1.86). Dashed lines represent 95% confidence intervals. For comparison, the observed resting (a) and traveling (b) rates as a function of vessel abundance are shown in the panels below.