DO CALVES MATTER?: THE EFFECT OF NUMBER OF BOATS AND MODE OF APPROACH ON THE BEHAVIORAL AND ACOUSTIC RESPONSES OF CETACEAN GROUPS WITH CALVES

By:

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GENERAL INTRODUCTION

Whale and Dolphin Watching

In 1994, the International Whaling Commission (IWC) made a resolution for a more sustainable use of cetacean resources due to population declines caused by whaling practices. This resolution resulted in whale and dolphin watching practices which have become one of the most common and profitable tourism activities worldwide. Since then, whale and dolphin watching activities around the world have been growing at a steep rate and have been of great economic impact for developing countries (O'Connor et al., 2009). Currently, whale and dolphin watching tourism takes place in 119 countries around the Globe with a total profit of over $2.1 billion USD. Cetacean tourism practices concentrate in North America, Africa and the Middle East, and Oceania with a recently growing effort in South and Central America (Hoyt and Iñiguez 2008, O'Connor et al., 2009). Because whale and dolphin watching is mainly boat-based, there is concern about the possible negative effects of the growing cetacean watching industry and the associated boat traffic. As a result, the IWC (1996) created a series of guidelines to provide protection to the targeted cetaceans. These guidelines specifically addressed the appropriate distances and maneuver of boat approaches, together with the appropriate conduct of whale watchers. Each country, however, has its own set of guidelines adapted from the IWC to their own specific cases (e.g. Marine Mammal Protection Act, 1972). Enforcement of the laws for whale and dolphin watching is also case specific with some countries being stricter with regulations than others.

Whale and dolphin watching practices occur in different modalities that, in many cases, include prolonged and frequent interactions with boats (Erbe 2002). In addition, a wide range of numbers of boats can be interacting with cetaceans simultaneously and without resting periods between approaches. Constantly pursued by boats, cetaceans tend to respond altering their behavior patterns. Examples of responses are changes in behavior budgets (Lemon et al, 2006, Williams et al. 2006, Arcangeli and Crosti, 2009) and diving times (Nowacek et al. 2001). In addition to alteration of behavior, the motors of the vessels produce a broadband frequency noise that overlaps with the communication signals of most cetaceans which has the potential to hinder the communication with conspecifics (Jensen et al. 2009) during important biological situations such as group cohesion, contact between mothers and calves, and mating (Tseng et al. 2011).

Short-term effects of cetacean watching have been well documented (Nowacek et al. 2001, Constantine et al. 2004, Lusseau 2006, Arcangeli and Crosti, 2009), but information about long term impacts on the population level remains scarce (Trites and Bain 2000, Kingdom et al. 2007).. A few cases suggest that after long term exposure to anthropogenic activities, some populations abandon their habitat (Rowntree et al. 2001, Morton & Symonds, 2002, Bejder et al. 2006). To understand the potential long term effects of human disturbances the Population Consequences of Disturbances (PCoD) model was modified from the Population Consequences of Acoustic Disturbances (PCAD) model (Figure 1) proposed by the NRC (2005). The PCoD is a conceptual model that connects the disturbance to the decline of a population through a series of possible impacts of behavior changes to vital rates such as reproduction success, calf mortality rates, death rates, and ultimately population growth. Because reproductive success and calf mortality greatly depend on the behavioral responses of mothers and calves to human disturbances, it is necessary to directly study the impact of whale watching on such groups. Calves could be at higher risks of collisions with boats (Wells and Scott, 1994) possibly because of curiosity, feeding behaviors, socialization, inexperience around the boats (McFee et al., 2006), and inexperience of nursing mothers (Nowacek et al., 2001). In the case of bottlenose dolphins, calves stay with their mothers for 3 to 5 years (Mann & Smuts 1998; Mann et al., 2000) and their survival depends on the condition of their mothers, experience, and foraging success (Mann & Watson-Capps, 2005). If reproductive success of females is compromised by exposure to dolphin-watching vessels (Bejder, 2005) it is necessary to pay special attention to how tourism is affecting mother-calf pair interactions, behavior of groups with calves, and calf survivorship; especially for small resident populations.

Bottlenose dolphins and dolphin-watching in Bocas del Toro

The Bottlenose dolphin (family: *Delphinidae, Tursiops* spp.) is a cosmopolitan species living in a wide range of habitats around the world (except for Polar Regions). Two ecotypes have been identified as inshore and offshore according to the species distribution (Caballero et al., 2011). Inshore dolphins typically live in coastal habitats where they can be long-term residents, while offshore populations have a wider habitat range and live in deep oceanic habitats. Coastal populations tend to be small and show high site-fidelity and low genetic variability (Natoli et al. 2004), which makes particularly vulnerable to changes in habitat and incidental mortality due to fisheries and boat collisions (Wells & Scott 1999; Reeves et al. 2003).

Bottlenose dolphins live in fusion-fission societies where group membership shifts constantly. Nonetheless, they do show strong social bonds such as mother and calf pairs that can last between 3-5 yr (Connor et al. 2000), and male alliances that could last a lifetime (Watwood et al.

2004). Social bonds are reinforced by physical (Dudzinski, et al. 2010) and acoustic communication. Bottlenose dolphins produce a variety of sounds that range from broadband pulse sounds to tonal whistles. Experiments in both captivity and the wild suggest that whistles are used as cohesion calls (Janik and Slater 1998) and under context-specific situations (Janik and Slater, 1998). These communications calls are learned by the calves who model their "vocal" repertoire from the signals of their conspecifics (McCowan and Reiss 1995, Quick and Janik 2008). When separated from their mothers, calves emit whistles repeatedly to contact their mothers and initiate reunion (Smolker et al. 1993).

Many studies have looked at a variety of responses to boat presence that include changes in inter-breath intervals (e.g. Nowacek et al. 2001), direction and speed of traveling (e.g. Constantine et al. 2001 and 2004), behavior budget (e.g Lusseau 2003) as well as acoustic communication signal frequency shifts (May-Collado and Wartzok 2008) and emission rate (Buckstaff, 2004). Although the short-term effects on behavior have been examined, little is known about the potential long-term effects at the population level (Lusseau, 2006). It has been suggested that extensive exposure to anthropogenic disturbances can drive a population to abandon their habitat. For example, Bedjer et al. (2006) found that the relative abundance of bottlenose dolphins in Shark Bay, Australia is reduced in areas where vessel activity due to dolphin watching tourisms is higher. Not all populations, however, face the same level of boat traffic, or have the option to disperse to quieter habitats.

One of the greatest concerns regarding dolphin interactions with boats is how mothers with dependent calves respond to boat approaches and how these dynamics can influence the survival of the calves. While it has been suggested that boats should never approach a group with calves

(IWC, 2006), it is a practice that is commonly observed in the field. Some studies suggest that females with dependent calves show different avoidance strategies to boat approaches. For example, females with dependent calves seem to engage in traveling behavior more often when approached by boats, possibly limiting their available time to nurse their calves (Slensland and Berggren, 2007). When boats are already too close to the females, the chances of collisions increase as they are unable to synchronize with the rest of the group in vertical avoidance behaviors (or prolonged dives) (Tseng et al. 2001). In addition, the increased underwater noise caused by the engine noise can potentially mask whistles (Jensen et al., 2009) which are important communication signals between mothers and calves.

In the case of Bocas del Toro, Panamá, dolphin-watching is one of the main tourism activities, and possibly represents a great percentage of the total tourism profit. The bottlenose dolphin population of Bocas del Toro has been studied since 2004. A total of 169 individuals have been marked with photographs of natural marks in their dorsal fin, which are specific for each individual (Würsig and Jefferson 1990, May Collado et al. 2007). Of these, it is likely that less than 20% are year-round residents, particularly of the bay known as Dolphin Bay, where the dolphin-watching concentrate their tours, due to the high predictability and availability of dolphins. This bay is also the area where there seems to be a higher concentration of mother-calves pairs per group, highlighting the importance of the bay as nursing ground. Previous studies have found that dolphins that inhabit the bay respond to the dolphin-watching by shifting whistle frequency from low to high frequencies and by lengthen their signal duration, presumably as an strategy to reduced masking and enhance signal transmission (May-Collado & Wartzok 2008). Although boat traffic does not seem to play a major role in determining dolphin presence, largely due to their dependence on this habitat for reproduction and foraging, it does affect their behavior during the interaction (Taubitz 2007, Barragán-Carrera 2010). Dolphins tend to spend more time traveling and under water when many dolphin-watching are following the group (Barragán-Carrera 2010) and this tendency is reinforced particularly when the boats are aggressively following the group (circling the group, rapid approaches with sudden changes of speed) (Taubitz 2007). Because these practices are considered unsustainable (Lusseau et al. 2006) the Panamanian government has implemented guidelines to regulate the behavior of the operators while interacting with the dolphins (Resolution ADM/ARAP NO. 01). The guidelines clearly state that dolphin-watching boats should stay at a minimum distance of 100m, or 250m for groups with mother-calf pairs. The maximum speed allowed in the area of dolphin-watching is four nautical knots (or 7 km/hr), and changes in speed is prohibited. It also stated that interactions should be limited to 30 minutes and a maximum of two vessels can be in a radius of 250m from the dolphins. These guidelines are not followed by most dolphin-watching operators. Instead, the aggressive approaches are becoming more common and it was evidenced by the death of three calves in 2011. All corpses showed markings of collisions with boats.

The goal of this thesis is to expand on the ongoing long term research of the bottlenose dolphin population of Bocas del Toro and the impacts of dolphin watching on their acoustic behavior. The main objective is to study how dolphin watching activities in Panamá could be disrupting the communication of bottlenose dolphins, in particular for groups where calves are present. Specifically, I will look at repetitions of communication signals as a way to increase the likelihood of conveying a message. First, I review how whale and dolphin watching has been studied for the past decades to look at differences in responses according to group composition (i.e. presence of calves). Then, I directly address the impact of dolphin watching tours on the whistle rate of bottlenose dolphin groups with and without calves looking at several factors that include number of boats and type of approach.

Do calves matter? Addressing the importance of including calf presence in the assessment of whale-watching impacts.

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The effect of whale watching on cetacean populations has been of popular concern since the whale watching industry increased dramatically during the past decade. Whales and dolphins show behavior and acoustic reactions to boat approaches that could potentially lead to a disruption of vital activities, and thus, vital rates of the populations. Unfortunately, the long term population consequences of behavior responses are yet to be understood. There are several factors that could influence how cetaceans respond to whale watching including the time of exposure, the activity budget, and the presence of calves. Calves have always been considered more vulnerable to interactions with whale-watching boats and their presence in a group could elicit different behavioral and acoustic responses from those of groups without calves. In this review I analyze the importance of including presence of calves as a factor influencing variation in responses to boat interactions by reviewing the evidence for differences in behavioral and acoustic responses. In many cases, studies are based on the average of behavioral responses and very few studies divide data by group composition (e.g. groups with mother-calf pairs). In the cases where groups' composition was considered, mother-calf pairs showed more

avoidance behaviors and more vulnerability to boat interactions. The information of acoustic responses of mothers and calves is limited, particularly for baleen whale species. However, vocalization rates vary among groups with and without calves, which represent a source of variation in the data for acoustic responses of a population to vessel noise. For these reasons, I recommend that the presence of calves be included as an important factor for future assessments of whale-watching impacts on behavior and acoustic responses. Adding this factor will refine the data and management can be targeted to more vulnerable groups.

INTRODUCTION

The effect of tourism on marine mammals has been a major focus of interest since the 1990's, when the whale-watching industry gained its momentum as a result of a resolution for a more sustainable use of cetacean resources by the International Whaling Commission (IWC, 1994). Observations of cetaceans in the wild rapidly flourished as a replacement for other uses of cetaceans generating great remunerations worldwide ($2.1 billion USD in 119 countries, (O'Connor et al., 2009) and rising concern about the welfare of cetacean populations. Many publications have discussed the short and long term consequences of whale-watching on cetaceans. For example, disruptions of biologically important behaviors such as feeding and socializing have been reported for several species including mysticetes (baleen whales) and odontocetes (toothed whales). Moreover, there are cases where populations shift patterns of habitat use in a disturbed area or even abandon it completely (Lusseau and Bejder 2007). Unequivocally, being constantly followed by boats trigger behavioral responses in cetaceans, however, whether or not such responses could hinder reproduction or survival, and ultimately affect the growth rate of a population is currently a matter of discussion among the scientific community. To understand the potential long term effects of human disturbances the Population Consequences of Disturbances (PCoD) model was modified from the Population Consequences of Acoustic Disturbances (PCAD) model (Fig. 1) proposed by the NRC (2005). The PCoD is a conceptual model that connects a human disturbance to the decline of a population through a series of possible impacts of behavior changes to vital rates such as reproduction success, calf mortality rates, death rates, and ultimately population growth.

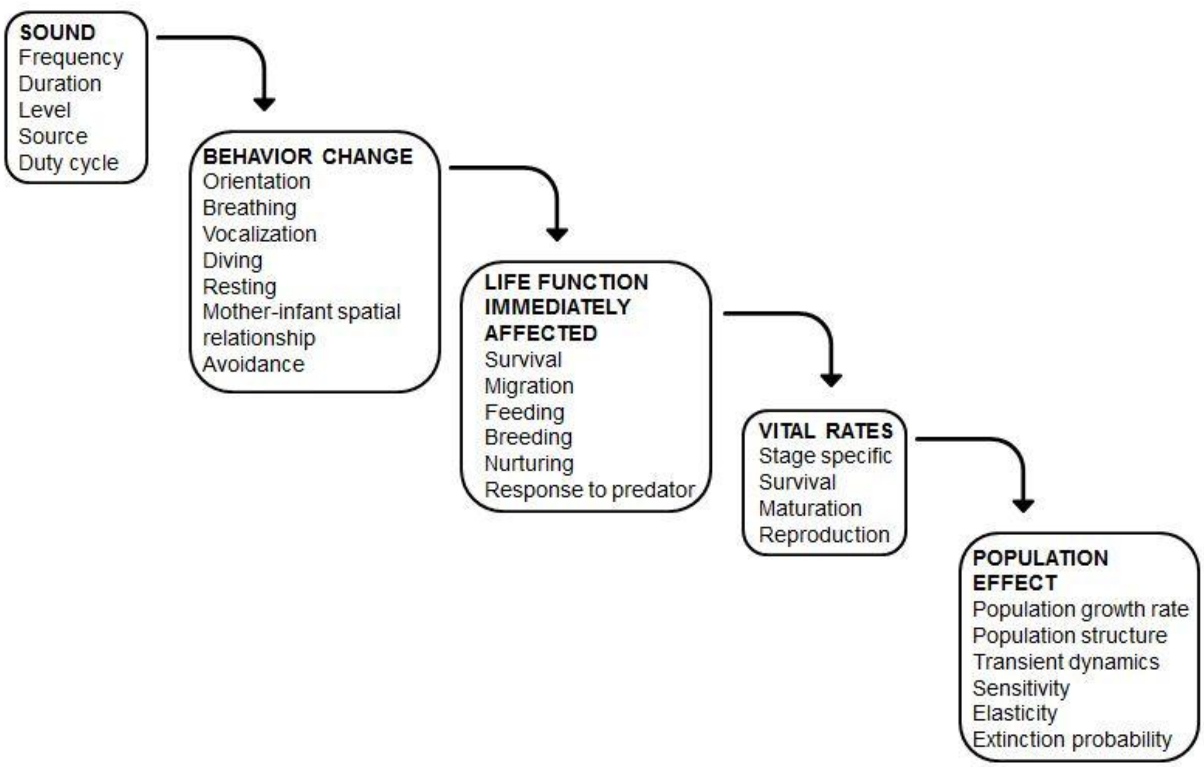

Figure 1. Population Consequences of Acoustic Disturbance adapted from NRC (2005).

Because reproduction success and calf mortality greatly depend on the behavioral responses of mothers and calves to human disturbances, it is necessary to directly study the impact of whale watching on such groups. Calves could be at higher risks of collisions with boats (Wells and Scott, 1994) possibly because of curiosity, feeding behaviors, socialization, inexperience around the boats (McFee et al., 2006), and inexperience of nursing mothers (Nowacek et al., 2001). In the case of bottlenose dolphins, calves stay with their mothers for 3 to 5 years (Mann and Smuts 1998; Mann et al., 2000) and their survival depends on the condition of their mothers, experience, and foraging success (Mann and Watson-Capps, 2005). If reproductive success of females is compromised by exposure to dolphin-watching vessels (Bejder 2005) it is necessary to pay special attention to how tourism is affecting mother-calf pair interactions, behavior of groups with calves, and calf survivorship; especially for small resident populations. In addition, nursing mothers could be incurring in a higher energetic cost by avoiding or interacting with tourism boats (Lusseau, 2003; Williams et al. 2006). Independently, most studies neglect the presence or absence of calves as an important variable influencing the variability of behavior and acoustic responses (Table 1). The latter could lead to misrepresentation of the behavioral responses of cetaceans to the vessels because it looks at the average response of a group or population (Williams et al., 2006) as it has been shown that mothers with calves and groups or pods containing calves could have different avoidance strategies to boat disturbances (Nowacek et al. 2001). These strategies could be related to the energy budgets of both mothers and calves (Williams et al. 2006), possibly affecting the survival and reproduction rates of the populations.

In this review I analyze the importance of including presence of calves as a factor influencing variation in responses to boat interactions by reviewing the evidence for differences in behavior and acoustic responses of groups with and without calves.

Table 1. Summary of published work on whale and dolphin watching showing the proportion of publications where calves are considered as a factor for changes in responses.

SPECIES	CALVES RESPONDED DIFFERENTLY	NO DIFFERENCE IN RESPONSE	CALVES WHERE NOT CONSIDERED
BEHAVIORAL RESPONSES			
Bottlenose dolphins (*Tursiops truncatus*)	Nowacek et al., 2001; Hastie, 2003; Lusseau 2003*; Akiyama et al. 2007		Acevedo, 1991; Constantine, 2001, 2004; Buckstaff, 2004*; Lusseau, 2004,2006; Mattson et al. 2005; Arcangeli et al. 2009, Mattson et al. 2005; Janik 1996)
Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)	Stensland and Berggren 2007; Hawkins and Gartside 2010		Lemon et al. 2009
Pantropical spotted dolphins (*Stenella attenuate)*	Montero-Cordero 2007		
Sotalia costero (*Sotalia guinensis)*	Santos et al. 2006	Filla and Montero 2009	
Common dolphin (*Delphinus delphis)*	Stockin et al. 2008		
Killer whale *(Orcinus orca)*	Williams et al. 2002*		
Irrawady dolphin *(Orcaella brevirostris)*			Hashim & Jaaman 2011
Chinese white dolphins *(Sousa chinensis)*			Hashim & Jaaman 2011
Risso's dolphin (*Grampus griseus)*			Visser et al. 2011
Humpback whales (*Balaenoptera novangliae*)	Schaffar et al., 2008; Stamation et al., 2010		
Gray whales (*Eschrichtius robustus)*			Heckle et al. 2003
Sperm whale (*Physeter macrocephalus*)			Richter et al. 2006
ACOUSTIC RESPONSES			

A. bottlenose dolphins (*Tursiops truncatus*)		Scarpaci et al. 2000; Akiyama 2007
Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)		Lemon et al. 2006
Chinese white dolphins *(Sousa chinensis)*	Van Parijs and Cockeron, 2001	
Killer whales *(Orcinus orca)*		Foote et al. 2004

*Did not take into account presence of calves, but made the distinction between males and females.

Behavior responses

Behavior state

Changes in behavioral states are one of the most studied responses to whale-watching. Researchers divide behaviors by categories according to function (e.g. feeding, diving, socializing) while at the same time these behaviors encompass other less frequent behaviors (e.g. tail slaps, jumps). Then, the frequency of the different behaviors or the behavioral transitions can be compared among boat traffic intensities or the observer can track when a change in behavior occurs as a consequence of boat approaches (e.g. Acevedo, 1991; Lusseau, 2004; Lemon et al., 2006; Arcangeli and Crosti, 2009). Consequences of changes in behavior include disruption of important behaviors such as feeding, socializing, and resting; although there is no clear evidence of how such disruptions would directly affect the vital rates of the population in the long term.

The PCoD model predicts that a reduction in feeding behavior could have a negative effect on the energy budgets of the individual animals as they are likely to spend their energy avoiding the vessels instead of replenishing their energy needs (Williams et al. 2006). Williams et al. (2006) estimated that the increasing traveling behavior accompanied by a decrease in feeding behavior of the killer whales (*Orcinus orca*) in Johnstone Strait, British Columbia, would cost them approximately 18% of their energy intake. For nursing mothers, this energy cost could be higher. The decrease of feeding behavior has also been observed in Indo Pacific bottlenose dolphins (*Tursiops aduncus*) (Steckenreuter et al., 2011) and bottlenose dolphins (Miller et al., 2008). Unfortunately, there is no direct evidence for the energetic costs of behavioral responses for mothers of any cetacean species and how these costs would affect the survival of the calf.

Calf mortality has been associated with tourism activities (bottlenose dolphins, Bedjer 2005; beaked whales, Weilgart 2007; humpback whales, Weinrich and Corbelli, 2009). Groups with calves could show a different response to tourism boats as females with dependent calves could maneuver differently to protect their young. For example, female bottlenose dolphins alone show a different response to boat approaches; they respond with longer dives while males swim away in a horizontal direction (Lusseau 2003). It is possible that the mobility of females could be hindered by the presence of calves, which could be misinterpreted as a lack of response or a positive response towards the boats. In addition, the natural curiosity of calves makes them approach vessels more often than individuals with more experience with boat traffic, possibly forcing the mothers to stay closer to their calves. For example, a study conducted in Praia de Pipa, Brasil showed that the species *Sotalia guianensis* responds differently to boat approaches if there were calves present in the groups (Santos et al., 2006). Groups with calves engaged in more socialization and displacement behaviors compared to groups without calves. This is partly consistent with the findings for bottlenose dolphins (Lusseau 2003, 2004; Stensland and Berggren 2007) where displacement behaviors were dominant in the presence of tour boats for females and groups with calves, respectively. The Pantropical spotted dolphin (*Stenenella attenuate*), was also found to engage in socializing behaviors more often in the presence of tourism boats, while resting and feeding activities were sighted more often when no tourism boat was present (Montero-Cordero, 2007). For this study they only encountered a group with calves in three occasions, and noticed that the mothers slapped their tales in the presence of the control boat, and not the tourism boats. Stensland and Berggren (2007) reported that Indo Pacific bottlenose dolphin females with dependent calves seem to engage in traveling behavior more often when approached by boats, possibly limiting their available time to nurse their calves. Another study reported that bottlenose dolphin females with calves have greater chances of collisions with boats as they are unable to synchronize with the rest of the group in vertical avoidance behaviors (or prolonged dives) (Tseng et al., 2001). Bottlenose dolphin mothers also showed less resting and more traveling when tourist boats were present in a population of Zanzibar, East Africa. The same pattern was observed for Risso's dolphins (*Grampus griseus*) and bottlenose dolphins where their resting pattern decreased during the peak hours of dolphin watching (Visser at al., 2011) and interactions with swimmers (Constantine, 2004).

Studies that do not separate their targeted groups by presence and absence of calves sometimes record behavior changes that may not seem to be of biological importance (e.g. Lemon et al. 2006) which could be perceived as a non-threatening interaction between dolphins and boats. In their study bottlenose dolphins change behaviors from traveling to milling and then back to their original travel path after the interaction with the passing vessel. This is probably an evidence of acclimation to boat traffic or an average response of groups that does not take into consideration more vulnerable members of the population.

Speed and direction of movement

When pursued by boats, cetaceans can increase their speed and change the direction of their traveling path to avoid interacting with boats. For mothers with dependent calves, increasing their speed could mean a higher cost of energy and the possibility of leaving their calf unattended, although evidence is needed. On the contrary, changing the direction of the movement to avoid vessels could be a more common strategy. For example, Williams et al. (2002) reported shifts in speed and swimming angle that were markedly different for killer whale females. In the case of humpback whales, changes in direction of movement were observed more often for groups that were not accompanied by calves, while groups with calves preferred a more vertical type of avoidance (Stamation et al., 2009). The consequences of deviating from the traveling pathway could be detrimental to migratory species as humpback and gray whales since they need to return to their feeding areas before exhausting their energy reservoir. In the case of non-migratory species, changing the direction of their swim could extend their foraging period (Janik, 1996). Once again, energy exhaustion and replenishment becomes the main issue for this type of response and the impact of such responses on nursing mothers remains unknown.

Inter-breath intervals

Another strategy to avoid vessels is spending less time in the surface (Wells and Scott, 1997). Scientists classify this time as the inter-breath intervals (IBI) or vertical avoidance (Lusseau, 2003) compared to horizontal avoidance (i.e. change in direction). For example, a population of bottlenose dolphins residing in Sarasota Bay showed longer IBI in the presence of passing vessels (Nowacek et al., 2001). They also found that IBI was longer for experienced mothers than inexperienced mothers and females without calves, meaning that with experience, mothers have learned to avoid vessels by staying underwater for longer periods. This avoidance behavior has been observed across isolated populations and it was also observed for bottlenose dolphins in New Zealand (Lusseau, 2003) where females also spent more time underwater than males. Mother-calf pairs could be more vulnerable to be struck by boats because the presence of the calf could hinder its mother’s maneuverability (Wells and Scott, 1997; Nowacek et al., 2001). The effect of longer inter-breaths intervals on oxygen intake needs to be further studied to address the true costs of this avoidance strategy. In addition, not taking into account group composition of the population under study could lead to a misinterpretation or underestimation of the real vertical response to boat approaches.

Swimming synchrony

Swimming synchrony or breathing synchrony has also been included in the repertoire of cetacean behavioral responses to whale watching. Most of the studies reporting a change in swim synchrony did not make the distinction between groups with and without mother and calf pairs (e.g. Hastie et al., 2003; Miller et al., 2008; Tosi et al., 2009). However, for bottlenose dolphins, the presence of calves typically decreases the synchrony of the groups (Hastie et al., 2003; Stamation et al., 2008) meaning that for this particular behavior it is important to control for the presence of calves.

Baleen whales

Mother-calf pairs of baleen whales are easier to detect in the wild because they travel in pairs (Thomas and Taber. 1984), making them an easier target for whale-watchers. For humpback whales, research on the short-term effect of whale-watching boats always separated groups according to presence or absence of nursing females. Short-term behaviors that vary depending on the presence or absence of nursing females included changes in respiration rate, time spent submerged (Stamation et al., 2010), and swimming speed (Schaffar et al., 2008). Weinrich and Corbelli (2009) looked at the effect of whale watching on calf production and survival rate of humpback whales in Southern New England and found no relationship between the two. However they admitted that their study only considered mother-calf pairs that made the migration to the feeding grounds, and therefore, underestimated the real number of calves born. In addition, whale-watching also takes place in the breeding grounds of this population, which should be included in a future assessment of calf survival. For other Mysticete species information about short-term behavior reactions to whale-watching boats is scarce. Gray whales (*Eschrichtius robustus*) didn't show any response to whale-watching vessels when traveling in their southbound migration (Heckle et al., 2003). However, they noticed that whales changed traveling direction in presence of boats during the northbound migration. In this case gray whales migrate from Canadian waters to the Baja California to breed and give birth, which means that the northbound migration had a greater chance to be accompanied by calves. This was not mentioned in the study, but could be a plausible explanation for the observed change in behavior.

Acoustic responses

The underwater noise produced by the engines used in tourism vessels can potentially mask the communication signals of cetaceans (Richardson, 2005; Jensen et al., 2009), but some species can adapt their acoustic behavior to compensate for the loss of transmission of their calls and songs (Foote et al., 2004: Nowacek et al., 2007). These adaptations include increasing their call redundancy (Buckstaff 2004), or the duration (May Collado and Wartzok, 2008), amplitude (dB) (Holt, 2009) or the frequency (Hz) (Akiyama et al., 2007) of the calls to avoid masking. Recently, studies of the energetic costs of changing vocal behavior are emerging to address the consequences on the individuals energy budget (e.g. Jensen et al., 2012). The consequences of not being heard could have a negative impact on the population level if disruption of communication leads to a decrease in reproductive activities or if a mother loses contact with her calf which would put them both in a vulnerable situation.

In order to understand the effect of the vessels' noise on calf survival, it is important to determine if the noise has the potential to disrupt the communication between the mother-calf pair and how groups with calves or mother-calf pairs respond acoustically. For example, groups with calves in whistle producing odontocetes tend to have a higher vocalization rate than groups without calves in the presence of boats (Van Parijs and Cockeron, 2001: Hawkins and Gartside 2010). Specifically, Pacific humpback dolphins (*Sousa chinensis*) showed that groups with calves had a significantly higher whistle rate when a vessel was passing than groups with not calves (Van Parijs and Cockeron, 2001). Furthermore, they show that whistle rate increases with the number of calves in the group. When groups are divided by the presence or absence of calves, the results are more representative of the real responses of cetaceans to boat disturbance.

In contrast, when presence of calves is not considered in the data analysis, it is likely that the acoustic response observed corresponds to an average of whistle production. That is probably the case for Indo Pacific bottlenose dolphins (*Tursiops aduncus*), in which group composition was noted during the field collection but not considered in the data analysis (Lemon et al., 2006). Their results showed that vocal production of resident travelling bottlenose dolphins was not affected by the presence of powerboats. However, for the same species it has been shown that groups with and without calves differ in whistles production (Hawkins and Gartside, 2010), meaning that for this case, it is unknown whether or not the presence of powerboats affects the vocal production according to group composition. For cases where management decisions are needed, results showing no response could be misinterpreted as lack of disturbance.

In the case of baleen whales, very little is known about the vocal production and the hearing capabilities of neonates and older calves. Recently, it was confirmed that calves of humpback whales off Hawaii produce calls that are different from adult calls and songs (Zoidis et al., 2008). These calls are low in amplitude, which implies they are more prone to masking. More information is required to address the impact of whale watching on the communication between mothers and calves and how it may affect the survival of the individuals.

CONCLUSION

Measuring the impacts of cetacean watching is moving towards more empirical data with the emphasis of modeling its long term consequences in cetacean populations. Important long term consequences are shifts in habitat use and declines in the population stocks which are particularly emphasized for small isolated populations. Population declines in cetacean populations are often associated with decreased reproduction rates and high mortality rates of calves. Although small populations are subject to declines due to stochastic events, anthropogenic disturbances can aggravate the vulnerability of such populations due to the combination of added negative effects. For this reason, it is important to assess the impacts of whale watching to determine which responses are of biological significance to the life history of the populations.

Short-term behavioral responses do not translate directly to effects at the population level (Gill et al., 2001), but with the advances in the conceptual models of PCAD and PCoD, it is possible to predict what behavioral changes could lead to a vital impact on individuals and focus future research on studying that connection and the consequences for the wealth of the populations. I suggest that future impact assessment focus their attention on how behavioral changes of mother-calf pairs affect the survival rate of calves, and its impact on population growth. As exposed here, most behavioral and acoustic responses to whale watching can vary according to the presence of calves, which needs to be taken into account for future studies on the impact of whale and dolphin watching.

Dolphin-watching boat activity influence dolphin communication: the effect of number of boats and mode of approach on whistle emission rate

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Unregulated dolphin watching activities has been shown to negatively affect resident dolphin populations worldwide. In recent years a number of regulations have been put in place to reduce potential negative impact by controlling the number of boats interacting with dolphins at a giving period of time and by setting norms of conduct for the operators. Although several studies have evaluated the impact of number of boats on dolphin acoustic behavior, little is known on how the way boats approach dolphins may affect their behavior and communication. In Panama, a small resident population of bottlenose dolphins (*Tursiops truncatus*) in Bocas del Toro is regularly subject to dolphin watching activities. Dolphins are under constant presence of multiple boats (up to 37) and tend to be approached at high speeds and at close proximity creating a vulnerable situation for the dolphins, particularly for groups with calves. We made the assumption that these types of aggressive approaches can elicit an acoustic response; specifically we

expected an increase in whistle rate for interactions that could represent a higher noise level. We expected this response to be higher when calves are present because they require being in contact with their mothers. Our results showed that groups with calves decreased their whistle rate in presence of boats, while groups without calves increased their whistle rate. At the same time, when boats were present, whistle rate was significantly higher during aggressive interactions compared to passive interactions (p=0.009), particularly for groups with calves. Our results show that the mode of approach may have negative effects on dolphin communication. In addition, because mothers and calves are in need of contact, the presence of calves in a group maybe an important factor influencing whistle rate. A reduction on mother-calf communication in the presence of boats can make calves more vulnerable to boat strikes, which have been documented in this population, and consequently have a negative impact on the growth of the population. Finally, we highlight the urgent need for enforcement of the cetacean observation guidelines in Panamá not only on number of boats but also modes of approach.

INTRODUCTION

Whale and dolphin watching in Latin American countries have contributed to the economic growth of developing coastal areas that previously depended on unsustainable fishing (Hoyt and Iñiguez, 2001). However, this transition from fishing to whale watching was not necessarily accompanied by sustainable practices (e.g. Lusseau et al. 2006). Whale and dolphin watching in many areas grew as a free market where any owner of a vessel could practice cetacean observations without proper training and often without protective laws or enforcement of laws regarding cetacean welfare. While in

Latin America the industry of whale and dolphin watching is still developing and has been growing at high rates for the last decades, in other parts of the world, the negative consequences of whale and dolphin watching on the behavior of cetaceans, and ultimately its effects at the population level have been extensively studied (e.g. Mississippi Sound, US – Miller et al. 2008; New Zealand – Lusseau 2003, 2004, 2006; Sarasota Bay, Florida – Nowacek et al. 2001; Shark Bay, Australia – Bejder et al. 2006). There is consistency of negative consequences of whale and dolphin watching across populations for both short-term and long-term consequences. The short-term consequences of whale and dolphin watching include changes in behavior state (Acevedo, 1991, Lusseau 2004, Lemon et al.2006, Steckenreuter et al. 2012), longer dive periods (Janik 1996, Nowacek et al. 2001), changes in swim speed and pattern (Hastie et al. 2003, Stensland and Berggren 2007), death by boat strikes (Wells and Scott 1997, Lusseau 2003) and changes in the emission of communication and echolocation signals (Scarpaci 2000,Van Parijs 2001, Foote et al. 2004, Lemon et al. 2006, Akiyama and Ohta, 2007, May Collado and Wartzok 2008, Díaz López, 2011). Examples of long term consequences include abandonment of critical habitats (Cope et al. 2005, Bejder et al. 2006) and changes in reproductive success (Weinrich and Corbelli, 2009).

The effects of whale and dolphin watching can be divided into two main categories: the direct physical impacts and the acoustic impacts. The physical impacts (i.e. collisions with boats) can be lethal, but the noise produced by the vessels has a less obvious negative effect. Before a vessel approaches a cetacean individual or groups, it is first heard a couple of hundred meters before it is close enough for recreational observation activities, thus the acoustic interaction occurs prior to a close contact. Because bottlenose dolphins (*Tursiops truncatus*) depend on sound to communicate, the noise produced by boat engines can potentially shorten dolphins' communication range (Southall 2004, Jensen et al. 2012) for the period of the disturbance, and mask their communication signals (Richardson 1995, Janik 2000, Southall 2004). Therefore, the main concern about the impacts of whale and dolphin watching lies on the acoustic disturbance. Short-term reactions to acoustic disturbances do not imply a major effect on the survival or fitness of an individual or population and therefore, it is necessary to create models to determine if a type of noise disturbance is of biological significance (Bejder et al. 2006, NRC, 2005). Nevertheless, if communication is interrupted between a mother and her calf, both the mother and the calf could be more vulnerable to boat strikes which are common in areas of high boat traffic where the victims of collisions with boats are often calves (Wells and Scott, 1997). The probability of calf mortality due to boat strikes is also associated with the experience of the mother (Lusseau 2003) and her capability to stay in close contact with her calf.

Because bottlenose dolphins (*Tursiops truncatus*) depend on sound to communicate, the noise produced by boat engines can potentially decrease their acoustic space (Southall 2004, Jensen et al. 2012) for the period of the disturbance. Interrupting the communication of individuals for a short period of time, as in the case of interactions with dolphin watching vessels, may not have a direct impact on their survival. Nevertheless, if communication is interrupted between a mother and her calf, both the mother and the calf could be more vulnerable to boat strikes which are common in areas of high boat traffic where the victims of collisions with boats are often calves (Wells and Scott, 1997). The probability of calf mortality due to boat strikes is also associated with the experience of the mother (Lusseau 2003) and her capability to stay in close contact with her calf.

Bottlenose dolphins in the Archipelago of Bocas del Toro, Panamá are exposed to daily interactions with dolphin watching boats. Panamá is a member of the IWC and has a political policy for whale-watching (Hoyt and Iñiguez, 2008). The policy document clearly states that approaching dolphins at a closer range than 100 m is prohibited, with a 200 m limit for groups with calves (Resolution ADM/ARAP NO. 01). In Bocas del Toro, approaches towards dolphins for purposes of dolphin watching often involve fast speed, close proximity (<5 m), as well as circling the dolphins regardless of the presence of calves. Most of the time, interactions of boats with dolphin involve more than 10 boats at a time for more than 1.5 hr which is a practice known to exacerbate the negative responses of bottlenose dolphins (Steckenreuter et al. 2012), suggesting it is unsustainable.

With the growing dolphin watching industry, more boats are engaging in dolphin watching activities increasing the levels of underwater noise inside the Dolphin Bay –the main resting and nursing habitat for this population (May-Collado et al. 2007). The underwater noise perceived by the dolphins could be aggravated by fast speed approaches at close distances (Erbe 2002, Southall 2005). This could be particularly important for mother-calf pairs if they become acoustically separated during an aggressive interaction with boats.

Here we investigated if aggressive boat approaches elicit a higher emission rate of whistles relatively to non-aggressive approaches. We made the assumption that aggressive approaches represent relatively higher underwater noise levels compared to approaches that follow the dolphin watching guidelines (i.e. slow speeds, engine off, and more than 20 m away from dolphins) because the noise created by the engine increases with changes in speed (Erbe 2002). We expected that dolphins will response to the increase in underwater noise, with an increase in communication signals based on previous studies on bottlenose dolphins (Scarpaci et al. 2000, Buckstaff 2004), humpback whales (Miller et al. 2000), and Pacific humpback dolphins (Van Parijs et al. 2001). During boat approaches, mother-calf pairs could be more interested in maintaining contact, thus increasing the redundancy of their calls if the sound is masked by the engine noise (Richardson 1995, Southall 2004). In addition, considering that noise produced by boat engines at higher speeds and closer proximity could potentially mask the whistles (Erbe 2002, Steckenreuter et al. 2011), we expected that dolphins will increase their whistle emission rate to compensate for the possible masking effect.

METHODS

Study area and species

Bottlenose dolphins (*Tursiops truncatus*) are the only cetacean species found in the Dolphin Bay at the Archipelago of Bocas del Toro; a bay characterized by shallow waters (<20m) and variable bottom substrate (mud, coral, sea grass, and mangroves) located in northwestern Panamá (9°13' N, 82°14' W)(Fig. 1). Because of their high fidelity to this site (confirmed by photo-identification collected from 2004 to 2012), bottlenose dolphins are subject to an increasing dolphin-watching industry. Moreover, the population seems to be small, consisting of transient dolphins and a very small number of residents. First estimations of the population size using photo-ID concluded that the overall population of bottlenose dolphins in Bocas del Toro was around a hundred individuals (May-Collado et al. 2007). However, during our last survey in 2012 the same three groups consisting of a total of 27 dolphins were consistently sighted inside the Bay and the surrounding areas suggesting that the population of residents have decreased in the last eight years. This decrease is consistent with the increase in the number of boats interacting with dolphins (5±3 boats for 2004 and 9±7 boats in 2012). Although the Panamanian government recently decreed regulations to control for this activity and protect the species involved, dolphin-watching in Bocas del Toro remains unregulated, meaning that any number of boats can interact with the dolphins at any distance and speed without incurring in penalties. Frequently, the boat drivers will create waves by traveling in circles around the dolphins at fast speeds, and because most of the time dolphins ride the waves or jump, this practice is viewed by the community as a playful interaction. The peak of these interactions between dolphins and tour boats occur mainly between 9 am and noon, with overlapping interactions of ~30 min per tour boat.

Figure 1. Bocas del Toro is an Archipelago located in the located in northwestern Panamá (9°13' N, 82°14' W).

Surveys

Acoustic and behavioral data were collected from non-systematic surveys using a 25' boat with 45 hp engine. A group was defined as all dolphins within a radius of 400 m from our research boat whether or not they were engaged in the same behavior. Presumably, all these dolphins were within their acoustic space and detection capacity of our recording system.

Acoustic recordings

Acoustic recordings were collected using a RESON hydrophone 4033 (-203 dB re 1 V/lPa, 1 Hz to 140 kHz; RESON Inc., Goleta, California) connected to an AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400–500 kHz, 16 bit; Avisoft Bioacoustics, Berlin, Germany) that sent the signal to a computer for storage while displaying the signal waveform (May-Collado and Wartzok, 2008). Recordings were made continuously in 3 min files for the field collections of 2007 and 2008, while in 2012 recordings were made continuously in 1 min files. To avoid the effect of noise from our vessel, the engine remained off during data collection. In addition, recordings started after a period of 5 min of acclimation. Recordings ended when the dolphins were out of sight for more than 6 min or farther than a radius of 400 m. The 6 min interval threshold was selected because it represents the maximum diving time observed for this dolphin population (personal observation).

Dolphins' Surface Behavior

Simultaneously with acoustic recordings, the surface behavior of the dolphins was recorded from scan samplings of the group (Altmann 1974, Mann 1999) for every minute of the acoustic files that were recorded. Behaviors were divided into "resting", "traveling", "diving", "socializing", and "milling" as described by Lusseau (2004) (Table 1). When dolphins were out of sight for less than six minutes, the assumed behavior was "diving" unless the dolphins were seen performing the same behavior before and after a dive; in that case, the behavior before and after the dive was assigned to the recording. Together with surface behavior, we also collected the exact location and time of encounter, group size, and group composition (e.g. number of calves, group's membership -known dolphins from previous photo-identification).

Vessel approach surveys

Ideally, received noise levels should be measured or estimated in order to determine if the communication signals are being masked by the engine noise. However, the case of dolphin watching in Bocas del Toro consists of many possible scenarios of acoustic interactions between dolphins and boats; therefore, we decided to categorize the relative level of exposure to noise according to the number of boats at a given time and the type of approach.

Table 1. Description of behavior states by Lusseau (2004).

State	Definition
Resting	Group is moving steadily in a constant direction slower than the idle speed of the observing vessel. Swimming with short, relatively constant, synchronous dive intervals. Individuals are tightly grouped.
Traveling	Group is moving steadily in a specific and constant direction faster than the idle speed of the observing vessel. Swimming with short, relatively constant dive intervals. Group spacing varies.
Diving	Direction of movement varies. Group dives synchronously for long intervals. All individuals perform "steep dives," arching their backs at the surface to increase their speed of descent. Group spacing varies. Diving most likely represented the "feeding" category in other studies (Shane 1990).
Socializing	Many diverse interactive behavioral events are observed, such as body contacts, pouncing, genital inspections, and hitting with tail. Individuals often change position in the group. The group is split in small subgroups that are spread over a large area. Dive intervals vary.
Milling	Direction of movement varies. Group dives synchronously for long intervals. All individuals perform "steep dives," arching their backs at the surface to increase their speed of descent. Group spacing varies. Diving most likely represented the "feeding" category in other studies (Shane 1990).

Acoustic and behavior data was collected under presence and absence of boats. At the same time boat approaches were divided into three main categories according to aggressiveness towards the dolphin group being the 1st category the most aggressive with fast speeds and close approaches, and the 3rd category the least aggressive according to the Panamanian guidelines for dolphin watching (Table 2). A boat was considered "present" when it was within a radius of 400 m of the dolphin group or when it was first audible in the recordings. Discrimination by audibility was only possible for single boat approaches or when multiple boats were present and only one boat was approaching the area while the others were in constant speed or their engine was off.

Table 2. Description of types of approaches

Type of approach	Description
1	Aggressive. Boats approaching dolphins at high speeds, perpendicular to the dolphins' swimming direction, and/or circling the group. Closer than 10m.
2	Close approaches (<10m), changes in speeds towards the group. Low speed.
3	Non aggressive. Parallel approach at distances greater than 20m. Slow speed or engine off.

Number of boats was divided into six categories. Zero boats represents when only the research boat was present. The other categories were divided as: 1-3 boats, 4-6, 7-9, 10-12, and 13 or more boats. The 13 or more boats category ranged from 13-17 boats with an average of 14 boats. We did not know how many boats had their engines off at a given time, thus it is possible that type of approach, instead of number of boats would be a best estimate of the relative noise exposure.

Whistle rate

The acoustic recordings were catalogued using Raven Pro 1.4 (2011; The Cornell Lab of Ornithology) with a fast Fourier transform size of 1,024 points, an overlap of 50%, and using a 512- to 522-sample Hann window. We calculated whistle rate for every recording collected in absence or presence of boats. To take into account the differences in recording time, number of whistles was divided by the time of each recording. In addition, group size was considered in the calculations of whistle rate because previous studies suggest that whistle rate is proportional to the number of individuals in a group (Quick and Janik 2008). Whistle rate was then calculated as whistle count divided by the number of dolphins divided by time of the recording.

Statistical analysis

Non-parametric statistics were used because the distribution of whistle rate was skewed towards zero and did not follow normality even after transformation. Because in many occasions we recorded the same groups due to the size of the population in Bocas, the best statistical approach was to use repeated measures; therefore we used the Friedman test to compare whistle rate between presence and absence of boats. The same test was used to compare whistle rate among behaviors and to test whether the presence of calves influenced the acoustic responses of dolphins to boat presence. Individual comparisons by groups were performed using a Wilcoxon pair test. Statistical tests were performed using software R version 2.11.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) and Statistica Academic software (StatSoft, Canada).

RESULTS

Whistle rate was not significantly different when compared between recordings in which boats were present and absent (Mann Whitney U-test $X^2 = 2210$, p-value = 0.070). When presence of calves was added into the analysis, whistle rate was significantly different when compared between presence and absence of boats (Friedman's $X^2 = 73.91$, df= 3, p-value = 0.000), with a higher increase in whistle rate in groups without calves in the presence of boats (Fig. 2).

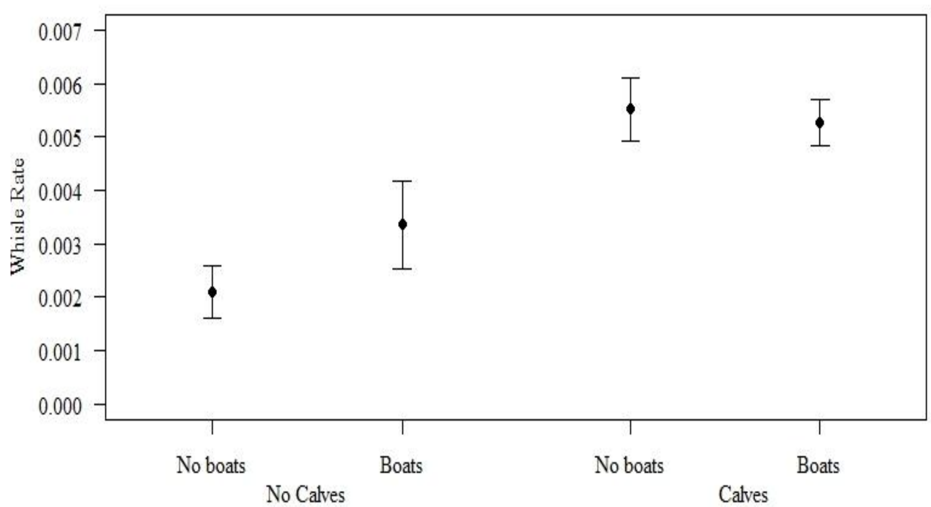

Figure 2. Groups with and without calves responded differently to presence of boats (Mean ±SE). Groups with no calves had a higher whistle emission rate ($p < 0.05$) while groups with calves had a significant lower emission rate ($p < 0.05$).

Whistle rate varied significantly according to number of boats (Kruskal Wallis' X^2= 13.58, df= 5, p-value = 0.018) with a peak in the boat category of 7-9 boats for both groups with and without calves. Whistle rate also varied significantly according to the type of approach (Kruskal Wallis' X^2= 11.93, df=2, p-value = 0.003) for groups with calves and not significantly for groups without calves (Kruskal Wallis' X^2= 4.40, df=2, p-value = 0.110). The sample size of the most aggressive approach (1) was small, and thus it was grouped with approach type number two. Fig. 3 shows the comparison between aggressive approaches (types 1 + 2) and non-aggressive approaches (type 3). Regardless of presence of calves, whistle rate was the lowest when boats approached dolphins in the least aggressive mode. Table 3 contains a summary of the collected data with the numbers of recordings used for each analysis.

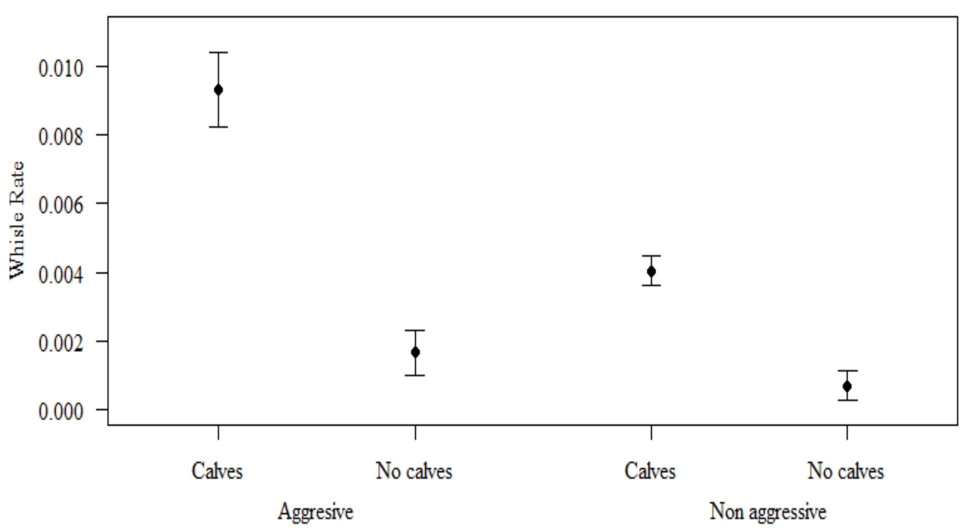

Figure 3. Mean ±SE values for the non-aggressive (type 1+2) vs. aggressive approach (3) showed a significant lower whistle rate (p = 0.009) for groups with calves. Groups without calves did not vary significantly between types of approaches.

Table 3. Data collection summary

Variable	
A. Summary of focal follow data	
Mean dolphin group size	6±5
Number of group follows	81
Focal follow hours	44
B. Summary of recording analysis	
Number of acoustic recordings	1184
Number of recordings of interactions with boats	731
Number of recordings with calves present	860
Number of recordings used for approach analysis	470
Number of recordings used for behavior analysis	907

Behavior

Whistle rate was higher in the presence of boats for all behavior categories (Friedman's X^2 = 44.20, df = 7, p-value = 0.000). Particularly, whistle rate was significantly higher during traveling (p-value = 0.04) states when boats were present (Fig. 4). Diving, milling, and socializing were not significantly different between presence and absence of boats (p-values = 0.122 and 0.354 respectively). The data from resting behavior was eliminated from the analysis due to the small sample size.

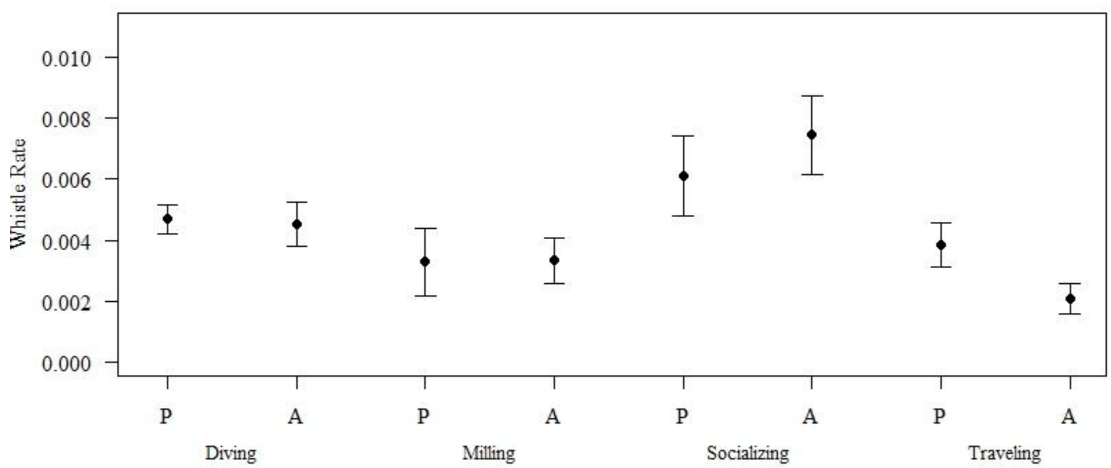

Figure 4. Traveling elicited a significant higher whistle emission rate ($p<0.05$). It is possible that the increase in whistle rate is a response to the masking effect of engine noise which is particularly important for behaviors that require group cohesion.

DISCUSSION

Several factors can influence the decision of vocalizing at a higher rate. In this study, both the presence of calves and the aggressiveness of the boat approaches influenced dolphin whistle rate. The purpose of our research was to determine the effect of dolphin-watching on the whistle emission rate of bottlenose dolphins, but because did not account with the necessary equipment to do experimental approaches, it was not possible to assess the noise levels received by the dolphins. To compensate for this, we categorized the situations in which noise level should have been different. The number of boats might give us the idea of the relative levels of noise (i.e. the higher the number of boats, the louder the background noise). The aggressiveness of the approach, on the other hand, could be a more accurate relative measure of noise.

Presence of boats

In our study we show that the presence of boats alone did not have an effect on the whistle emission rate of dolphins. We compared recordings when boats were and were not present. However the recordings that were used for the <absence> category include recordings from before and after the interactions with boats grouped together. It is possible that the time for acclimation after an interaction with a boat was not enough and instead, we recorded a delayed effect of the acoustic response. Other studies have addressed this by dividing whistle rate into larger categories that include the sequence <before>, <during>, and <after> an interaction with boats. For example, for bottlenose dolphins in Sarasota Bay whistle emission rate was higher during the onset (before) of the approach (Buckstaff, 2004). However, in our study area, approaches occurred simultaneously with the presence of other vessels, and interactions of various numbers of boats lasted up to two hours, making it difficult to follow the sequence protocol used by Buckstaff. Instead, we concluded that presence and absence categories were more appropriate for the circumstances of our study regardless of the sequence in which they occurred.

Approaches by dolphin-watching vessels can be seen as stressful situations for bottlenose dolphins and it may explain the observed increase in whistle emission rate in our study. Previous studies have shown that stressful situation may also influence emission rate (Esch et al. 2009). However, a higher whistle rate during encounters with boats could also mean that animals are alerting other individuals or are maintaining contact with conspecifics during the disturbance. While stress could be a possible explanation, it cannot be confirmed without testing the changes in stress hormones in association with dolphin watching practices. In addition, there is also the possibility that dolphins could be repeating their calls in order to increase the probability of overcoming the masking effect of the engine noise (Buckstaff 2004; Cook et al. 2004; Jones and Sayigh 2002; Watwood et al. 2005).

Although we expected an increase in whistle rate during presence of boats, our findings were consistent with a previous study where Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) did not change their whistle emission rate in the presence of powerboats (Lemon et al. 2006). Our study and that of Lemon et al (2012) contrast with Van Parijs and Cockeron (2001) and Buckstaff (2004) which did find an increase in whistle emission rate during interactions with boats. This suggests that there could be geographical variation in responses to engine noise, there could be differences in acclimation to disturbance at the different sites, or there are additional factors that need to be considered when addressing this question. In the case of Lemon et al. (2006), they concluded that it was possible that visual contact was enough for the dolphins of Jervis Bay, Australia, and possibly did not rely on sound for communication as heavily as other populations in murkier waters. The bottlenose dolphin population of Bocas del Toro live in relatively clear waters; therefore, their hypothesis could be consistent with what we found in Bocas del Toro. The main contrast between the previous studies is the consideration of group composition (i.e. presence or absence of calves). Both Van Parijs and Cockeron (2001), and Buckstaff (2004) found differences in whistle rate because they targeted groups with calves.

The effect of calf presence in whistle rate

Mother-calf pairs could be more susceptible to interactions with boats (Wells and Scott 1997, Mann et al. 1998, and Steckenreuter et al. 2012), thus we tested if the acoustic response to boat interactions was different for groups with calves compared to groups without calves. We could not target specific mother-calf pairs because our acoustic recording equipment was not directional. Instead, we compared whistle rate between groups with and without calves. We expected whistle rate to be higher for groups with calves when interacting with boats. Interestingly, we found that instead, they had a significantly lower emission rate.

Analyzing whistle rate for recordings with and without the presence of boats only provides an average of the acoustic response which in our case did not seem to be significant. When the same analysis was performed for groups with and without calves, it showed that group composition could be a factor influencing the acoustic response to noise, and that when ignored, it could give the wrong impression of a lack of response. This is consistent with the findings of Van Parijs and Cockeron (2001) where groups without calves in presence of boats had a significantly higher whistle emission rate than groups with and without calves in the absence of boats.

Number of boats

The same pattern occurred when whistle rate was compared among categories of number of boats. For groups without calves, whistle rate did not vary according to number of boats, while it was significantly different for groups with calves with 7-9 boats being the category with the highest whistle rate. Groups with calves had higher whistle rates for all boat number categories; although a correlation between number of boats and presence of calves was not tested here. In addition, the high variation in whistle rate among boat categories could be a result of different approach mode, and therefore, approach mode could be a better way to estimate response than just the number of boats present.

Effect of aggressive approaches

Aggressive boat approaches, on the other hand, did elicit a higher whistle rate that was markedly significant for groups with calves. Averaging groups with and without calves in the same analysis would have resulted in a non-significant response of whistle rate. This suggests that during aggressive approaches, groups with calves increase their whistle rate to maintain group cohesion, but at the same time, groups with calves tend to have higher whistle emission rates overall.

Indeed, our results show that dolphins whistled significantly higher during the two aggressive types of approaches. For this analysis we did not consider the number of boats to be a good predictor of levels of disturbance by noise because we did not know when a boat's engine was off and because we considered that the most aggressive approach at a given time was having the most impact. In addition, multiple approaches of boats consisted of more than three vessels approaching at different speeds and distances to the dolphins. With the amount of variables influencing noise exposure, and thus acoustic responses, we assumed that having a large sample size would account for most of the situations in the field, making our selected approach types comparable. For example, for aggressive approaches, boats were close (<10m) to dolphin groups and cruising at high speeds. Even if there were more than five boats in the area simultaneously, a single boat behaving in a more aggressive manner could have a larger impact on the noise received by the dolphins close to that particular boat, but this is yet to be tested. Interestingly, aggressive approaches elicited a higher whistle rate than less aggressive approaches, which is consistent with the proposed hypothesis. If the boats were masking the communication signals of dolphins in situations where group cohesion is important, then increasing the number of calls could increase the probability of communication.

Behavior states

In the case of behavior states, whistle rate was significantly higher during interactions with boats for only traveling and diving behaviors, possibly because both behavior states require more group cohesion than milling and socializing where dolphins are more tightly close to each other. In addition, for the data set of 2012, we had up to 16 boats following dolphins at the same time, decreasing the chances of accurately estimating the behavior state of the dolphin groups, as they were not visible most of the time. This probably inflated the number of recordings where dolphins were in the “diving” state.

In conclusion, dolphin-watching activities in Bocas del Toro, particularly during aggressive approaches, triggered an increase of the rate of communication signals. In addition, dolphin groups with different compositions (i.e. with and without calves) showed a different acoustic response to the presence of boats and thus, needs to be considered for future studies to avoid mistaking the lack of apparent response with lack of disturbance. Finally, we suggest that future management plans consider the reality of the dolphin watching tourism in Bocas del Toro to enforce guidelines towards the reduction of number of boats interacting with dolphins simultaneously, as well as their mode of approach. In addition, we believe that groups with calves should not be approached at any times.

GENERAL CONCLUSIONS

Measuring the impacts of cetacean watching is moving towards more empirical data with the emphasis of modeling its long term consequences in cetacean populations. Important long term consequences are shifts in habitat use and declines in the population stocks which are particularly emphasized for small isolated populations. Population declines in cetacean populations are often associated with decreased reproduction rates and high mortality rates of calves. Although small populations are subject to declines due to stochastic events, anthropogenic disturbances can aggravate the vulnerability of such populations due to the combination of added negative effects. For this reason, it is important to assess the impacts of whale watching to determine which responses are of biological significance to the life history of the populations.

As exposed in the first chapter, most behavioral and acoustic responses to whale watching can vary according to the presence of calves, which needs to be taken into account for future studies on the impact of whale and dolphin watching. This was made evident in my study of the population of bottlenose dolphins in Bocas del Toro (Panamá), where the presence of calves played an important role in determining if whistle rate varied in the presence of boats. Ignoring the presence of calves could have resulted in the assumption that whistle rate was not affected by the presence of boats.

There are several underlying factors involved in the responses of cetaceans to anthropogenic disturbances, and most interact synergistically such as the presence and the speed of the approaching boats and the interest of the animals in the interactions.

Although short-term negative responses are common, they do not translate directly to effects at the population level (Gill et al., 2001). With the advances in the conceptual models of PCAD and PCoD, however, it is possible to predict what behavioral changes could lead to a vital impact on individuals and focus future research on studying that connection and the consequences for the wealth of the populations. I suggest that future impact assessment focus their attention on how behavioral changes of mother-calf pairs affect the survival rate of calves, and its impact on population growth

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