

!

"

Hansestadt Rostock,  
Januar, 2007

# \_\_\_\_\_ \$

Prof. Dr. Gerhard Graf  
Laura May-Collado







%

Whales and dolphins are increasingly the focus of boat based whale-watching activities especially in coastal environments.

I investigated and compared the circumstances under which boat traffic may impact the vocalization and behavior of bottlenose dolphins (*Tursiops truncatus*).

The research was conducted in two areas with different level of boat traffic. In Bocas del Toro a high level of boat traffic is found, while in Gandoca-Manzanillo boats are less frequently.

I analyzed a total of 448.88 min of acoustical data that were collected between June 2004 and September 2006 by biologists Laura May-Collado and Dr. Douglas Wartzok from the Marine Mammal Lab at Florida International University.

Whistles, whistle frequencies, pulsed sounds and combinations of pulsed sounds with whistles were counted before, during and after interactions with boats.

Duration, number of inflection points and harmonics, modulation and several frequency parameters were measured and analyzed between areas and before, during and after boat encounters.

A behavioral study of the bottlenose dolphin was conducted between April and October, 2006 in both areas with a special focus on interactions with boats.

In addition boat type, the approaching mode of the boat and the engine power of each boat that interacted with dolphins as well as the total number of boats present were recorded.

Whale-watching boats produced more negative responses of dolphins than any other type of boat because of frequent interactions, intrusive approaching modes and high boat numbers.

Dolphins were found to increase travelling during and after interactions with whale-watching boats in Bocas del Toro.

The production rate of special sounds did not vary between areas or before, during and after interactions with boats.

Whistle parameter did not differ significantly between areas before interactions with boats, but during encounters a shift in start and maximum frequency occurred in Bocas del Toro. Additionally a shift from downsweep to sine whistles appeared in Bocas del Toro when boats were present.

In general dolphins of Bocas del Toro were found to respond more sensitive to boats than dolphins of Gandoca-Manzanillo.

)' \*

In aquatic environments visual communication among individuals is difficult due to light attenuation with depth and high turbidity. As a consequence, numerous aquatic organisms (including cetaceans) rely on sound for communication and for active and passive monitoring of their environments (Richardson et al. 1995). Because cetaceans strongly rely on sound to communicate, orientate, and avoid predation, scientists are increasingly concerned with the harmful effects of engine noise on cetacean populations. Among the most direct acoustic threats to cetaceans, activities are specifically directed at them, such as whale-watching.

In marine environments whale-watching has become an important tourist industry in over 87 countries and territories which attracts more than 9 million participants a year (Hoyt, 2001).

On the one hand this has increased the public awareness of marine mammals and has offered scientists a new platform to study whales, but on the other hand there are possible detrimental effects on the whales (Erbe, 2002; Buckstaff, 2004).

Particularly coastal populations are more accessible to this activity (Buckstaff 2004).

Since most whale-watching is boat based (72%) this kind of whale-watching has contributed considerably to increasing noise levels in many areas (Hoyt and Hvenegaard, 2002).

Although some dolphins react positive to fishing boats (Durden, 2005; Leung Ng and Leung, 2003), there are many reports about boat strikes which caused serious injuries or even death in marine mammals like manatees or dolphins (Evans, 2006; Carrillo and Tejedor, 2006; Krebs and Rahadi, 2004; Yan et al. 2005).

But also behavioral alterations have been observed.

Cetaceans are known to prevent anthropogenic noise produced by acoustic harassment devices (Johnston, 2002; Olesiuk et al. 2002), wind power generators (Koschinski et al., 2003) or boats (Kammigan et al. 2006; Lusseau, 2005; Moore and Clarke, 2002).

Short-term behavioral reactions to boats are fleeing (Leung Ng and Leung, 2003; Nowacek et al., 2001), increased breathing synchrony (Hastie et al. 2003), extended diving times and less surfacing (Erbe, 2002; Krebs and Rahadi, 2004, Leung Ng and Leung, 2003; Lusseau, 2003, Moore and Clarke, 2002; Nowacek et al., 2001), the decrease of inter-animal distance, an increased swimming speed or directional changes (Nowacek et al., 2001; Richter et al., 2006).

All these reactions are similar to predator avoiding tactics (Weihs and Webb, 1984) and produce both stress and energetic losses (Lusseau, 2003).

It is also known that some cetaceans change their acoustic behavior in response to intensive boat traffic or other kind of noise. For example bottlenose dolphins (*Tursiops truncatus*) and humpback dolphins (*Sousa chinensis*) produced more whistles during or after boat presence (Buckstaff, 2004; Scarpaci et al., 2000; Van Parijjs and Corkeron, 2001).

While long-finned pilot whales (*Globicephala melaena*) increased whistle rate during and after the exposure to military sonar sound (Rendell and Gordon, 1999).

Au et al. (1985) reported of a beluga whale (*Delphinapterus leucas*), which was brought from San Diego Bay, California to Kaneohe Bay, Hawaii. The ambient source level in the Kaneohe Bay was 12-17 dB higher than in San Diego Bay. After the transportation the beluga produced louder sounds with higher frequency. Romanenko (2004) studied some acoustic reactions of a bottlenose dolphin and got similar results with higher frequency production and structural alterations in the echolocation clicks under the influence of noise.

### Main Objective

In my thesis I studied the acoustic behavior of bottlenose dolphins in Bocas del Toro (Panama) and the Wildlife Refuge of Gandoca-Manzanillo (Costa Rica).

To determine if whale watching boats produce different reactions than other vessels and to detect possible reasons, I also included boat types, boat approaching modes, engine types and total number of boats in this study.

To get a wider image of the situation and to interpret the acoustic results with a higher certainty I also measured the behavior of dolphins under the different influences.

### Specific Objectives

1. Describe and quantify underwater anthropogenic noise for each study site in terms of the number of boats, type of boats (e.g., fishing, whale-watching, private, transport, etc), type of engines, and type of approaches to dolphins.
2. To determine if whale-watching boats are more likely to produce behavioral changes or negative responses of dolphins than any other type of boat.

3. To determine if overall differences in underwater anthropogenic noise between sites influence dolphin sound production (e.g. whistles, pulsed sounds) and their acoustic structure (e.g., duration, maximum-minimum frequency)

### Expectations

1. I expected to find more boats, especially whale-watching boats, in Bocas del Toro, like the Wildlife Refuge of Gandoca-Manzanillo is of less touristic interest.

2. Whale-watching boats interact more intensive with dolphin groups.

In many areas whale-watching boats were found to produce more negative responses than other boat types because they stayed longer with the dolphin groups and used other approaching types (e.g. Janik and Thompson, 1996; Nowacek et al. 2001).

I expected to find more travelling and less resting during interactions with boats (Lusseau, 2004). Also fishes were found to react and avoid boats (Engas et al. 1995). Furthermore soniferous fish that are detected by passive listening were found to be prevalent in the diet of bottlenose dolphins (Gannon et al. 2005). So I expected a decline of foraging behavior during interactions with boats.

3. Longer whistles or pulsed sounds were found during stressful situations or noise exposure (Kilian, 1993; Van Opzeeland et al, 2005) and they are less likely to be masked during noise. I expected to find longer whistles with higher frequencies (Ansmann and Evans, 2006) and less frequency modulation (Morisaka et al. 2005) or more inflection (Ding et al. 1995) in Bocas del Toro, like it was suspected to be the area with higher level of boat traffic. Furthermore I suspected to find a higher amount of whistles, pulsed sounds and combinations of pulsed sounds and whistles during or after a boat has been present in both areas. Combinations of pulsed sounds and whistles were produced in Atlantic spotted dolphins (*Stenella frontalis*) during excitement or stressful situations (Herzig, 1996). While burst pulses (a type of pulsed sounds) were found to be produced in agonistic or aggressive behavior in bottlenose dolphins and Atlantic spotted dolphins (Blomqvist and Amudin, 2004; Herzig, 1996). I considered it possible to find agonistic behavior against boats or against conspecifics due to stress.

Since Central America is considered to be the second fastest growing area in the whale-watching industry adequate strategies to regulate the possible negative effects are needed.

With this work I would like to contribute to this item.

.’

.’)

In the cetaceans the species *Tursiops truncatus* belong to the family of Delphinidae, the biggest family of Odontoceti.

The bottlenose dolphins inhabit tropical and temperate waters throughout the world. They are often found in coastal waters but also have been seen in the open sea (Huggenberger and Benke, 2004; Fig.2.1).

*Tursiops truncatus* is gray colored with a clearer coloration at the stomach. The fin is sickle-shaped.

Adult length is from 2.5-3.8 m and weight vary between 150 and 650kg<sup>1</sup>.

The animals live solitary or in groups of 2 to 70 individuals (Huggenberger and Benke, 2004). But there have also been estimates of herds that contain up to 10 000 animals, but such large numbers should be considered cautiously, as they could be a sign of “observer on overload”(Scott and Chivers, 1990). Nevertheless there can be found very large groups, especially in the open water.

Their social structure is embossed by a fission-fusion system with short-term casual acquaintances lasting a few days with a smaller proportion lasting several years (Lusseau et al. 2005). While temporary parties often contained both males and females, long-term consistent associations have been found between members of the same sex (Smolker et al. 1992). If a dolphin joins a group depends on personal affinities to associates as well as on extrinsic factors like for example home range preferences (Lusseau et al. 2005).

Lusseau and Newman (2004) found a general assortative mixing of dolphins by sex and age, but this arrangement does not seem to be strictly.

In Western Australia there have been found organized groups of males who formed alliances of

---

<sup>1</sup> Origin: American Cetacean Society: <http://www.acsonline.org/factpack/btlnose.htm>

two or three individuals who consistently associated with each other and were stable over periods of several years. These male subgroups seem to be associations which are as stable as the association between mothers and their dependent offspring (Smolker et al. 1992).

Bottlenose dolphins are highly opportunistic feeders. They feed on different species of fish, cephalopods, crustaceans and molluscs (Huggenberger and Benke, 2004). There have been found differences in diet between years and geographical location as well as between males and females (Kovacic and Bogdanovic, 2006).

Based on Laura May-Collado (unpublished data), the bottlenose dolphins of Bocas del Toro form a very small population (probably less than 100 individuals) that live year-round in the area.

In Gandoca-Manzanillo, however, only a few bottlenose dolphins are consistently observed in the area. Based on photo-ID work, it appears that these bottlenose dolphins form part of large offshore populations.

In addition to *Tursiops truncatus* there are more dolphins living in the Costa Rican study site, of which the most common is the tucuxi (*Sotalia guianensis*).

*Sotalia guianensis* is also seen in mixed groups with *T. truncatus*.

There might be some differences between the Panamanian and Costa Rican population due to this mixed-species associations.

No dolphins from Bocas del Toro have been observed in Gandoca-Manzanillo or vice versa despite the short distance between these two sites.

.'. & 2 %

The study was conducted in two locations that vary in underwater anthropogenic noise levels.

% \$ located at the Caribbean coast of Panama, close to the Costa Rican border.

Rainfall is of approximately 2870 mm per year. The dry season and the rainy season are not clearly defined, but there are two seasons of low rainfall, in March as well as between September and October and two periods of high rainfall in July and December (Guzmán et al. 2005). Anthropogenic underwater noise in this study site comes from several sources:

the Almirante Port, private and different types of transport boats that travel from one island to the other, and whale-watching activities which have become popular in the province, and are concentrate in Bocas Torito. Bocas Torito is a small bay where dolphins appear to spend considerable time foraging and socializing. The bottlenose dolphin is the only resident cetacean species in Bocas (see section 2.1)

= .'. \$ Study areas Gandoca-Manzanillo (north) and Bocas del Toro (south) marked in red. The main study area in Bocas del Toro is Bocas Torito marked in orange.

# < \$ Located at Caribbean coast of Costa Rica, in the province of Limón. It is about 35km away from the study site in Bocas del Toro (Fig. 2.2). Unlike Bocas, anthropogenic underwater noise sources only include engine noise from sport fishing and whale-watching activities. Whale-watching activities are limited compared to Bocas. The yearly rainfall and other climatic factors are very similar (Herrera, 1985) and the rain and dry seasons are in the same months<sup>2</sup> than in Bocas del Toro.

So apart from differences in overall boat traffic these two habitats are relatively similar in several climatic and environmental factors.

---

<sup>2</sup> information of the meteorological national institute of Costa Rica

.’4 !

In Bocas del Toro data was collected during four boat-based surveys of ten days taking place in April, July, September and October 2006.

In Gandoca-Manzanillo surveys were accomplished during 12 days in May, June and September 2006.

Surveys were conducted from 7 am to 5 pm in Bocas del Toro and from approximately 8 a.m. to 4 p.m. in Gandoca-Manzanillo Panamanian time.

In addition, to the data collected in Gandoca-Manzanillo I included behavioral data collected by Biologists Laura May-Collado and Monica Gamboa-Poveda.

The surveys were carried out in a boat with a 40hp outboard engine and a 135hp twin engine in Bocas and Gandoca-Manzanillo, respectively.

When a group of dolphins was sighted, I noted the geographical position using a GPS (Garmin), the time at beginning and end of the encounter, behavior at the moment of the encounter, group size (minimum, maximum, and best estimation of number of dolphin in the group), composition (number of calves, juveniles and adults) and whether boats were present or not. A group was defined as an aggregation of individuals, showing different level of organisation in a limited area, which performs similar activities and was moving in the same direction (Wells et al. 1999).

Sampling was performed using the behavioral protocol of the Tucuxi-Bottlenose project by Laura May-Collado and Monica Gamboa-Poveda.

Instantaneous sampling of focal-group behavior was performed every three minutes (*sensu* Altmann, 1974). According to Shane (1990) this method best reflects dolphin behavior. In addition the two-dimensional geometry of dolphin groups based on Shane (1990) (Table 2.1)

.’)§ Geometries of the dolphin group according to Shane (1990).

	refers to dolphins less than one body length apart
/	designates a separation of greater than one but less than five body lengths
< 2	refers to individuals spread greater than five body lengths apart
>	means that group members are spaced irregularly in a combination of two or more of the previously defined geometries

was performed.

In an effort to avoid under- and oversample focal groups I only include groups in the analysis with a minimum of 20 minutes and a maximum of 2 hours of behavioral observations.

This protocol was followed in the presence and absent of boats. The behavior of the group was classified into six categories as defined by Shane (1990), Cubero-Pardo (1998), and May-Collado and Morales Ramírez (2005) as follows:

§

Moving steadily in one direction. In some cases travelling was combined with other activities like socializing, or foraging.

& §

All interactions between individuals consisting of rubbing (with flippers, the whole body or penducle), belly up swimming, persecutions between individuals, slaps against the surface, mother-calf interactions, areal behavior, exposing head or nose, pectoral flipper waving in the air, tail flukes waving in the air or sexual behavior.

Social behavior is often associated with splash caused by two or more dolphins in contact with one another. “Social splash” obscures the details of their interaction.

In interactions with a boat bow riding or inspection of the boat were also classified as socializing.

= §

Behavior from searching to prey catch and consumption. Dolphins that are alone or in loose or widely dispersed geometry, commonly diving repeatedly in varying directions in one location. The dives were characterized as fluke-up dives (dolphin exposes its flukes as it dives) or sometimes tail-stock dives (exposing the penducle but not the flukes).

In Gandoca-Manzanillo it was possible to see the dolphins hunting at the surface, characterized by sudden increment of speed. Sometimes it was feasible to see fleeing fish.

This kind of foraging was often linked with hunting birds, swimming or flying near the area of interest.

§

The animals are nearly immobile at the surface or are moving very slowly but without any specific direction.

§

Moving in varying directions in one location but showing no surface behaviors and no apparent physical contact between individuals. Animals are usual staying close to the surface.

! §

All individuals of the focal-group are under water for at least five second. Shorter diving times were regarded as surfacing (Leung Ng and Leung, 2003).

In addition to behavioral data information on boats and engines from both locations (especially Bocas where boat traffic is particularly high) was collected simultaneously.

The presence of a boat was defined if the distance between the boat and the dolphins was approximately 500m.

Boat type, power of engine, approaching mode and absolut number of boats present was collected.

Nine boat types were classified. Their descriptions are summarized in table 2.2.

The power of engine was obtained in the field from the inscription on the motor of interacting boats.

The way in which interacting boats moved was classified into ten approaching types summarized in table 2.3. A vessel was termed as fast if the bow was lifted out of the water.

The Number of boats that interacted with dolphins was collected. All boats that passed by or that stayed with dolphins were recorded.

.'. boat types observed in the study sites.

2	!
Research	Our boat used for investigation
Whale-Watching	Boats with tourists that stay and observe dolphins
Local Transport	Boats used for carrying passenger between islands or between mainland and islands, normally travelling at high speed
Personal	Boats primarily used for transporting workers and materials for work, as well as private vessels
Jetski	Fast motor-cycle like speed vehicles for one or two persons
Yacht	There was one private yacht in Bocas normally almost immobile doing whale-watching
Catamaran	Normally moving with inboard engine, doing whale-watching
Kayak	Without engine, often used from locals as fishing boats
Fishing boat	Small fishing boats with outboard engine

. '4\$ observed approaching modes of boats interacting with dolphin groups.

%	!
off	Engine off
0	Idle running
1	Fast, directed at the dolphin group, changes of speed
2	Fast, not directed at the dolphin group, changes of speed
3	Fast, directed at the dolphin group, no changes of speed
4	Slowly, parallel to the dolphin group, no changes of speed
5	Slowly, persecuting dolphin groups, changes of speed
6	Slowly, directed at the dolphin group, no changes of speed
7	Making circles
8	Fast, not directed at the dolphin group, no changes of speed

Finally, dolphins responses to boats was determined following Leung Ng and Leung (2003). The reactions of the dolphins to the boats were classified as positive, negative, and neutral (Table 2.4).

Table 2.4. Dolphin responses to boats

	Dolphin approach the boat, swim in the waves or follow it after it has passed by
	Dolphin flee or avoid the boat, radical behavioral changes, fast directional changes
	No observable changes of behavior, continue to perform ongoing behavior

The acoustical data was collected between June 2004 and September 2006 by biologists Laura May-Collado and Dr. Douglas Wartzok, from the Marine Mammal Lab at Florida International University in Bocas del Toro and Gandoca-Manzanillo.

Dolphins signals were recorded in the field using a broadband system as described by May-Collado and Wartzok (2007) were a RESON hydrophone (-203 dB re 1V /  $\mu$ Pa, 1 Hz to 140kHz) was connected to AVISOFT recorder and an Ultra Sound Gate 116 (sampling rate 400-500 kHz 16 bit) sent the signal to a laptop.

Table 2.5

It is important to note that not the real number of boats that occurred in the area was determined, but the number of boats that interacted with dolphins per minute.

So if a boat, like for example a whale-watching boat stayed several minutes with the dolphin group the number of boats per minute increased.

The average number of boats and boat types per minute in each area was calculated (Table 2.2).

In addition I determined the number of boats and boat types per minute in the morning (7am-12) and the afternoon (12:01pm-5pm) separately. Power of outboard engines of interacting

boats was subdivided into four power-classes: to 50hp, 51-100hp, 101-150hp and greater 150hp respectively. The percentage of boats with engines in the particular power-class was determined.

Again, not the real percentage of boats with engines in the particular power-class was calculated but the percentage of engines of boats that interacted with a dolphin group.

If a boat in a particular power-class stayed for several minutes, the percentage of the related power-class increased.

Responses were valuated using statistical test to determine if dolphins react more positive, negative or neutral depending on boat type, engine type, approaching mode or the total number of boats.

## 2 §

Data was arranged according to the boat types that occurred. Just data where one boat type (excluding the research vessel) was present was applied.

Then the reactions (positive, negative, neutral) of dolphins to each boat type was compared among one another.

## " 2 §

Data were divided into four power-classes: to 50hp, 51-100hp, 101-150hp and greater 150hp respectively.

Data where boats from just one power-class (excluding the research vessel) were present was considered.

The responses of dolphins to each power-class were compared among on another.

## % §

The research boat was always present, but we never moved in mode 1,2,3,5,7 and 8. Therefore data where our engine was off or idle running and another boat moved in another way were utilized for analysis. Significance was proved for individual approaching types as well as for

fast versus slowly, directed to the group versus not directed to the group and changes of speed versus no changes of speed.

Just contrast pairs were compared:

For the analysis of fast versus slowly, approaching modes 1,8,3 were compared with 5,4,6.

For the analysis of directed to group versus not directed to group, approaching modes 1,3,6 were compared with 2,8,4.

For the analysis of changes of speed versus no changes of speed, approaching modes 1,5,2 were compared with 3,6,8.

+ §

Data was organized by the specific number of boats that interacted with dolphins in one time interval and the reactions of dolphins were compared between specific boat numbers

Samples of boat type, engine type, approaching mode and the total number of interacting boats were considered to be independent because samples for each side of the test were taken from the dataset non-consecutively, from those points at which the special boat type, engine type, approaching mode or the specific number of boats occurred.

The responses of dolphins were analysed and evaluated statistically using a Kruskal-Wallis-H-test. In case of statistical significance, individual pairs were compared using a Mann-Whitney-U-test (Untersteiner, 2005).

Differences in the categorized approaching modes: fast versus slowly, directed to the group versus not directed to the group and changes of speed versus no changes of speed were proved using a Mann-Whitney-U-test.

Behavior and group geometry of encounters where we have been with dolphins before, during and after the presence of other boats were compared between different situations.

Because only a few encounters between dolphin and boats were observed in Gandoca-Manzanillo, this section consist exclusively of interactions of Bocas del Toro.

This data was analysed according to Lusseau (2006). The fact that during longer observation times the frequency of behavior increases and that the probability that more different specific behavior occurs if the group consists of more members was taken into account.

First counts in each category were normalized by sampling period and number of individuals (equation 1).

Where observing time refers to observing time before, during and after the presence of vessels respectively. To avoid overestimation of small focal groups the behavioral indice was then fourth root-transformed.

The two-dimensional geometry of the group was determined similar to the behavioral indice, but the group size was not taken into account because just one geometry could appear independent of the group size (Equation 2).

Because the same dolphin groups were measured at different times the behavioral indices and the indices of geometry before, during and after encounters with boats were tested for significant differences using the non-parametric Friedman-test for dependent samples (Untersteiner, 2005). Pairs were proved for differences by a Wilcoxon-test in case of significance.

It has been shown that there are differences in dolphin diurnal behavior (e.g. Cubero Pardo, 1998; May-Collado and Morales Ramírez, 2005; Shane, 1990). In addition, boat reaction may be dependent on dolphins' behavior at an specific time of the day (Shane, 1990).

So it seems to be important to compare general behavioral data variation between areas and time of the day to be able to interpret reactions to boats with more certainty.

Data was split into two time intervals. The first from 7 am to noon and the second between 12:01 pm and 5 pm. Just encounters without other boats was used.

Samples in each areas were considered to be independent because they came from several observations of different focal-groups. In addition group composition of bottlenose dolphins changed between days.

Differences were tested with a Mann-Whitney-U-test for two discrete and independent samples (Untersteiner, 2005).

!

A total of 448.88 min were analyzed using RAVEN 1.2 (Cornell Laboratory of Ornithology, New York) with a FFT size of 1024 points, an overlap of 50%, and a 512-522 sample Hann window. A total of 20 sequences (ten for each locations) of dolphin-boat interactions were analyzed.

" ! !

The total number of whistles, whistle – sequences, pulsed sounds and combinations of whistles with pulsed sounds was quantified for each area.

These sound types will be defined subsequently:

< \$

Whistles are narrow bandwidth, often frequency modulated tonal sounds which last from 0.5 to a few seconds and may have harmonic structure. They are omnidirectional. They are probably produced within the nasal passage and the diverticula of the odontocete head (Cranford, 2000).

The function is thought to be primarily social (Hermann and Tavorla, 1980).

Whistles were subdivided into six categories based on their frequency contour as described by (Barzua-Duara and Au 2002): constant frequency, upsweeps, downsweeps, concave, convex and sine whistles (Fig. 2.3).

a) constant whistle

b) upsweep whistle

c) downsweep whistle with 2 harmonics

d) concave whistle

e) convex whistle

f) sine whistle with 3 harmonics

= .4\$ Examples of whistle contours and whistle harmonics

Also the number of each whistle contours that was produced in each location was quantified.

In addition, whistles with and without harmonics were counted (Fig.2.3 c,f).

Successive whistles were considered to be individual whistles if one of the following criteria has been fulfilled (Bazúa-Durán and Au, 2002):

- a) the gap between them was larger than 200ms.
- b) the gap was smaller than 200ms, but larger than the duration of the whistles.
- c) there was at least a 3 kHz frequency difference between the ending frequency of the first and the beginning frequency of the subsequent whistle.
- d) the whistle was twice as intense as the next one.

Otherwise whistles were accounted to be sequences or click interrupted tonal sounds.

Click interrupted tonal sounds could be allocated to one of the six whistle contours explained before but had a gap other than the criteria defined by Bazúa-Durán and Au (2002).

Whistle sequences look more like consecutive whistles with a gap other than defined before.

Both cases were sometimes difficult to distinguish and classification seemed to be highly subjective. So both categories were counted together in the category “sequences”.

\_\_\_\_\_§ (also referred as burst-pulse sounds or burst pulses) (Fig. 2.4)

Pulsed sounds are pulses produced at rapid rates (Cranford, 2000). They are so fast, that our ear is not able to dissolve the single pulse anymore and so they seem to be tonal to us. Some terms for pulsed sounds are moans, barks, squeaks or squawks. But the terms are rarely explicitly defined, so the choice of terminology is likely related to the subjective experience of the reporter (Cranford, 2000). Boisseau (2005) performs a good overview of synonyms used for the same sound type in the literature. Pulsed sounds are directional sounds with probable social function (Blomqvist and Amudin, 2004).

\_\_\_\_\_§

Combinations were defined as pulsed sounds with overlapping whistle contour as demonstrated in Figure 2.4.

= .6\$ Examples of pulsed sounds (left) and combination of pulsed and whistle (right).

For each of the 20 sequences of dolphin-boat interactions the quantity of sound types per minute and individual was counted.

In Gandoca-Manzanillo bottlenose dolphins are often found in mixed groups with the Guyanese dolphin (*Sotalia guianensis*). Guyanese dolphin whistles usually were shorter, with higher frequency and simpler contour than those produced by bottlenose dolphins. Thus it was possible to distinguish them in mixed-species recordings. But it was not possible to discriminate pulsed sound from different species.

So I used individual number of bottlenose dolphins in a group to calculate the whistles per individual and minutes, while for pulsed sounds total individual number of the mixed-species group was used.

Differences between Bocas del Toro and Manzanillo were proved by a Mann-Whitney-U-test for discrete and independent samples.

In addition I calculated the number of different whistle types, pulsed sounds and pulsed-sound-whistle combinations before, during and after the encounters with boats for each study site separately as well as between study sites.

Just sequences were recording started before the arrival of a boat were used. This was applied

for nine sequences in Bocas del Toro and for seven sequences in Gandoca-Manzanillo.

To determine if there were significant differences in sound production before, during and after I used the non-parametric Friedman-test for discrete, dependent samples within study areas and the Mann-Whitney-U-test for discrete, independent samples between areas (Untersteiner, 2005).

In addition I compared situations where boats has been present versus the absence of boats. All 20 sequences were interactions with boats and hence could be included.

To determined is sound production vary in the presence and absence of boats I used the Wilcoxon-test and the Mann-Whitney-U-test for samples within and between study sites, respectively

Whistles for acoustical measurements were selected based on the following properties (Bazúa-Durán and Au, 2002):

- a) a good signal to noise ratio
- b) clear in the overall contour shape, especially in their beginning and ending points
- c) either nonoverlapping or overlapped with at most two other whistles
- d) not evidently cut by the upper frequency limit of the recording system.

From each whistle the following parameters were extracted: (1) minimum frequency, (2) maximum frequency, (3) delta frequency, (4) start frequency, (5) end frequency, (6) peak frequency, (7) duration, (8) number of inflection points, (9) number of harmonics and (10) the coefficient of frequency modulation (COFM) according to Morisaka et al. (2005).

All parameters are explained in table 2.5 and / or figure 2.5.

Parameters 1-7 and 10 were manually extracted using the measurement tools of RAVEN 1.2 software.

RAVEN 1.2. has no feature to assess the start and the end frequency. So the peak frequency at the start and the endpoint was calculated instead.

.7\$ calculated whistle parameters and explanation.

?	!
Maximum Frequency	Highest frequency in the whistle
Minimum Frequency	Lowest frequency in the whistle
Delta Frequency	Frequency range – difference between maximum and minimum Frequency
Start Frequency	Frequency with which a whistle begins – here calculated as the peak frequency at the beginning of a whistle
End Frequency	Frequency with which a whistle ends – here calculated as the peak frequency at the end of a whistle
Peak Frequency	Frequency with the highest energy (highest amplitude)
Inflection points	Changes in the slope of the whistle from + to – and / or – to +
COFM	Expresses the degree of frequency changes in a whistle

= .7\$ nine of ten parameters measured for each whistle and the contour shape.

To determine the coefficient of frequency modulation the whistles were divided into 19 equal time intervals and 20 frequency points were determined using the peak frequency at each point. Then following equation (3) was used to calculate the coefficient of frequency modulation for each whistle:

where  $Y_n$  is the frequency at the  $n^{\text{th}}$  frequency point (McCowan and Reiss, 1995).

If the whistle has greater frequency modulation the value of the coefficient of frequency modulation increases, and vice versa.

Whistles that were calculated before, during and after the presents of boats belonged to different sequences, and concerned to be independent. Hence differences in the 10 parameters in each area were proved by a Kruskal-Wallis-H-test.

To determined if dolphin whistle acoustical parameters vary between sites and in the presence and absence of boats a Kolmogorov-Smirnov-test for parameter 1-7 and 10 was used.

Parameter 8 and 9 are discrete parameters. So they were compared by a Mann-Whitney-U-test.

**4'**

**4') &**

In the surveys between April and October I observed the bottlenose dolphin for actually 146.15 hours. 10.1 % of the observing time was spent in Gandoca-Manzanillo, where it was more difficult to find the dolphins and 89.9 % in Bocas del Toro.

Sighting distribution for the study period in both areas can be observed in figure 3.1a-b.

a) Bocas del Toro

b) Gandoca-Manzanillo Wildlife Refuge

= **4')§** Total sightings of dolphins in Bocas del Toro and Gandoca-Manzanillo. Both maps show the geographical positions of the groups at the moment of their encounter (bottlenose dolphin groups = red dots, Mixed-species groups= green dots)

#### 4'. %

Boat interaction rate was 0.66 and 0.21 boats/min in Bocas del Toro and Gandoca-Manzanillo respectively. Approximately, in Bocas del Toro one boat passed by every 1.5 minutes and every 4.8 minutes in Gandoca-Manzanillo. In addition, in Bocas del Toro the highest number of boats present in a dolphin sighting that was nine whereas the maximum in Gandoca-Manzanillo was three .

In Bocas del Toro the boat number varied clearly during the day. In the morning there were found almost three times more boats than in the afternoon (0.89;0,32boats/min). Especially the whale-watching boats arrived more in the morning. There were found almost six times more whale-watching boats in the morning than in the afternoon . In Gandoca-Manzanillo no evident variations were found (0,19;0,24 boats/min). In the afternoon slightly more boats were found in Gandoca-Manzanillo than in Bocas del Toro (Table 3.1).

4')\$ quantity of boats per minute in the both study areas, subdivided into boat categories. There have been observed a total of 0,66 boats/min in Bocas del Toro and 0,21 boats/min in Gandoca-Manzanillo. In both areas boats for whale-watching have been identified to be the most important boats which interact with dolphins. There are more different boat types in Bocas del Toro than in Gandoca-Manzanillo.

		< <	=	/		= 2	@ A	B	,
	morning	0.7165	0.0013	0.0186	0.0616	0.0006	x	0.0071	0.0885
	afternoon	0.1209	x	0.0029	0.0870	x	0.0077	0.0058	0.0957
	total	0.4784	0.0008	0.0123	0.0716	0.0004	0.0031	0.0065	0.0913
	morning	0.1818	0.0101	x	x	x	x	x	x
	afternoon	0.2234	0.0213	x	x	x	x	x	x
	total	0.1952	0.0137	x	x	x	x	x	x

Whale-watching boats were the most common type of boat in both study sites.

Bocas del Toro had the higher variety of boats which included local transport, personal boats, ferries, yachts and other boats (motorized catamaran, boats with inboard engine and kayaks).

In Gandoca-Manzanillo, apart from whale-watching artisanal fishing boats and sport fishing boats were sighted.

Fishing boats were sighted more often in Gandoca-Manzanillo than in Panama (Table 3.1).

However, in Bocas del Toro boat engines had greater power (mainly 50-150 hp) than in Gandoca-Manzanillo (mainly less than 50 hp Table 3.2).

4.3.2. Percent of boats in different engine power classes observed in the two study sites. Boats with smaller engines find more favour in Manzanillo than in Bocas del Toro.

	7: 000	7: 000-1000	1000-1500	1500-2000	2000-3000	3000-4000
	23.69	65.54	3.45	3.18	1.40	2.75
	57.63	29.66	12.71	0.00	0.00	0.00

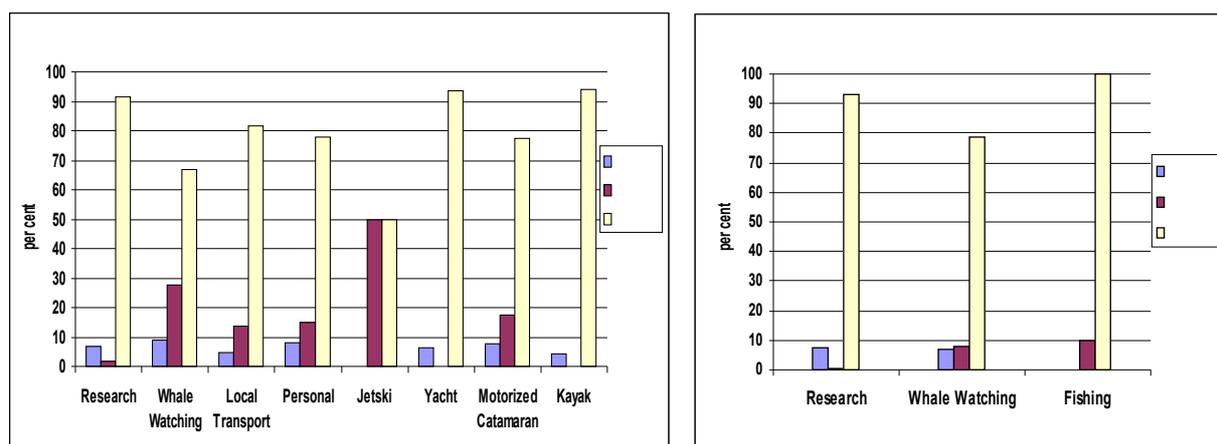
#### 4.4

!

In Bocas del Toro a total of 1006 responses to boats were recorded, excluding the research boat. Of these responses 78 were positive, 213 negative and 715 neutral. A Kruskal-Wallis-test indicated that negative and neutral responses were significantly associated with boat types (negative:  $\chi^2 = 398.718$ ,  $df = 7$ ,  $p > 0.001$ , neutral:  $\chi^2 = 227.606$ ,  $df = 7$ ,  $p > 0.001$ ).

It is important to note that neutral reactions were the most common reactions to all boat types, suggesting dolphins may be habituated to a certain level of boat disturbance.

There were no significant differences between positive, negative, and neutral reactions of bottlenose dolphins to whale-watching boats, and those of motorized catamaran and local transport ( $\chi^2 = 4.024$ ,  $df = 2$ ,  $p = 0.134$ ) (Fig.3.2).



4.3.2. Reaction to different boat types in Bocas del Toro (left) and Gandoca-Manzanillo (right).

In Bocas del Toro whale-watching boats, motorized catamaran and local transport had a similar effect. Personal boats were less intrusive than whale-watching boats. In Gandoca-Manzanillo. There were just few interactions with other boats. Whale-watching boats and fishing boats produced the same percentage of negative reactions.

Note: Sometimes some members of the dolphin group reacted different than others. So total reaction to a boat type can be more than 100%

However, bottlenose dolphins did react less negatively and more neutral to personal boats than to the whale-watching boats (negative: Mann-Whitney-U = 29436.5,  $Z = -2.886$ ,  $p = 0.004$ , neutral: Mann-Whitney-U = 29927.5,  $Z = -2.410$ ,  $p = 0.016$ ).

The absolute number of negative responses to whale-watching boats was high due to their frequent interactions with dolphins ( $n = 165$  77% of all negative responses). Though there were a lot of positive responses ( $n = 52$  67% of all positive responses) to whale-watching boats the negative responses predominated.

In one occasion a jetski interacting with dolphins could be observed. It was the strongest negative reaction observed in this study. Dolphins fled very fast with directional changes and long dive times. But because of their higher abundance other boats are more important.

Dolphins responses to kayaks or the yacht did not differ from situations where just the research vessel was present ( $\chi^2 = 1.320$ ,  $df = 2$ ,  $p = 0.517$ ). No negative response was associated with them.

In Gandoca-Manzanillo a total of 119 responses to boats were recorded, excluding the research boat. Of these responses 8 were positive, 8 negative and 100 neutral. Statistical analyses indicated that negative and neutral responses were associated with boat type (Kruskal-Wallis-test to negative:  $\chi^2 = 22.547$ ,  $df = 2$ ,  $p > 0.001$ , neutral:  $\chi^2 = 6.170$ ,  $df = 2$ ,  $p = 0.046$ ).

Additionally to whale-watching boats just fishing boats were found to interact with dolphins.

No significant difference between reactions to fishing boats (negative=1; positive=0; neutral=10) and whale-watching boats (negative=9; positive=8; neutral=100) ( $p > 0.05$ ) was found (Fig. 3.2).

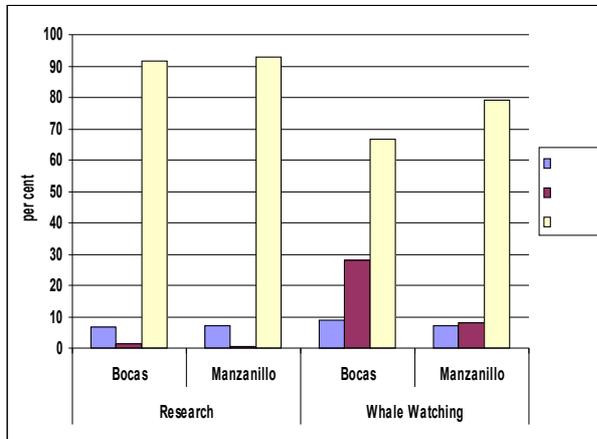
However, fishing boats normally were motionless and likely to be ignored by dolphins. Just in one occasion a negative response was found while the boat moved to another fishing site.

Comparison of the responses to the research vessel in Bocas del Toro and in Gandoca-Manzanillo was without distinction (Mann-Whitney-U = 237802.5,  $Z = -1.677$ ,  $p = 0.094$ ).

But there was a significant difference between the reactions to whale-watching boats (negative: Mann-Whitney-U = 25138.5,  $Z = -4.2$ ,  $p > 0.001$ , neutral: Mann-Whitney-U = 25185,  $Z = -3.916$ ,  $p > 0.001$ ). In Bocas del Toro bottlenose dolphins reacted more sensible to whale-watching boats than in Gandoca-Manzanillo.

Or with other words, whale-watching boats in Bocas del Toro seemed to be more intrusive than

those of Gandoca-Manzanillo (Fig. 3.3).



44\$ comparison of dolphins reaction to different types of boats. There was no significant difference in the reaction to the research boat, but there was a significant difference in the reactions to whale-watching boats. Whale-watching boats in Bocas del Toro seem to be more intrusive than those of Gandoca-Manzanillo.

# !

No significant difference of dolphin reactions to engine types between areas was detected (Table 3.3). So I combined datasets.

Dolphins reacted different depending on the power of the boat (Kruskal-Wallis-test: positive:  $\chi^2 = 1.257$ ,  $df = 3$ ,  $p = 0.739$ ; negative:  $\chi^2 = 85.324$ ,  $df = 3$ ,  $p > 0.001$ ; neutral:  $\chi^2 = 31.760$ ,  $df = 3$ ,  $p > 0.001$ ).

44\$ Mann-Whitney-U-test: comparison of reactions to different power of engine between areas.

7:	Mann-Whitney-U = 47262 Z = - 0.351 p= 0.725	Mann-Whitney-U = 47056 Z = - 0.653 p = 0.514	Mann-Whitney-U = 44972 Z = - 1.480 p = 0.139
7) )::	Mann-Whitney-U = 5539 Z = - 0.484 p= 0.629	Mann-Whitney-U = 5587.5 Z = - 0.225 p= 0.822	Mann-Whitney-U = 6282 Z = - 0.035 p= 0.972
)::) 7:	Mann-Whitney-U = 203.5 Z = - 0.927 p= 0.354	Mann-Whitney-U = 185.5 Z = - 1.938 p= 0.053	Mann-Whitney-U = 218 Z = - 0.089 p= 0.929

Dolphins reacted more negatively towards boats that used engines with power higher than 50 hp (Fig. 3.4).

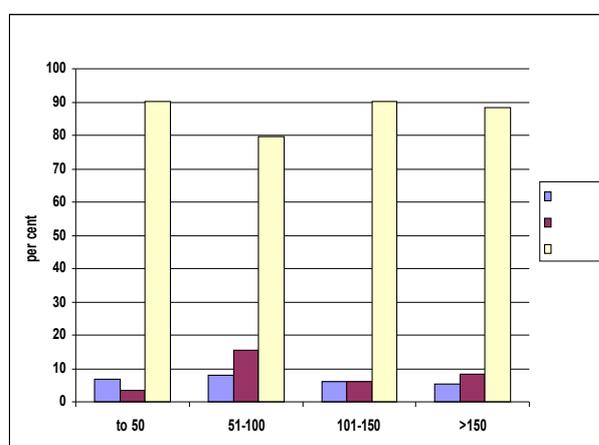
However, it is important to mention that sample size for engines with power between 101 and 150 hp was limited ( $n = 8$ ).

There were no significant differences in dolphin reaction to any other engine type ( $p > 0.05$ ).

Therefore, it is not possible to be certain of their perturbing effect on dolphins. Furthermore, the detrimental effect of vessels did not increase with engine power steadily.

Dolphins reacted more negative to engines of 51-100 hp than to engines with less than 50 hp (Mann-Whitney-U = 287947.5,  $Z = -9.271$ ,  $p > 0.000$ ) or to engines bigger than 150 hp (Mann-Whitney-U = 33806,  $Z = -2.445$ ,  $p = 0.014$ ).

These results suggest that factors other than engine power are more important for dolphin reaction (e.g., how boat approach to the dolphins or stroke of engines) and that significant differences are an aftereffect. Sample size need to be increased to compare boats that moved in the same way, but had engines with different engine power and those that have the same engine power, but differing strokes.

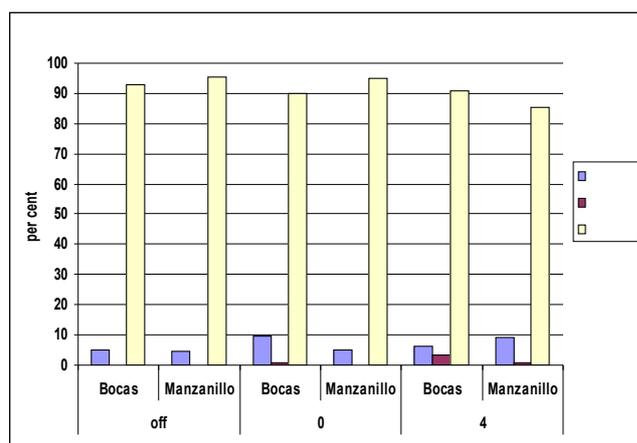


= 4'6\$ comparison of reactions of dolphins to boats with different engine power. The probability that dolphins react negative is highest with boats of 51-100 hp, followed by boats with more than 150 hp and less than 50 hp.

In both study sites there was a significant influence of boat approaching mode on bottlenose dolphin reactions (Kruskal-Wallis-test: Bocas: positive:  $\chi^2 = 140.393$ ,  $df = 9$ ,  $p > 0.001$ , negative:  $\chi^2 = 612.794$ ,  $df = 9$ ,  $p > 0.001$ , neutral:  $\chi^2 = 498.607$ ,  $df = 9$ ,  $p > 0.001$ , Manzanillo: positive:  $\chi^2 = 4.289$ ,  $df = 3$ ,  $p = 0.232$ , negative:  $\chi^2 = 126.743$ ,  $df = 3$ ,  $p > 0.001$ , neutral:  $\chi^2 = 32.558$ ,  $df = 3$ ,  $p > 0.001$ ).

Approaching modes 1,2,3,5,6,8 could not be valuated for Gandoca-Manzanillo because of their occasional occurrence.

Between areas there was not found any significant difference if the engine was off, idle running or if the boat was moving slowly without changes in speed and parallel to the dolphin group (Table 3.4, Fig. 3.5).

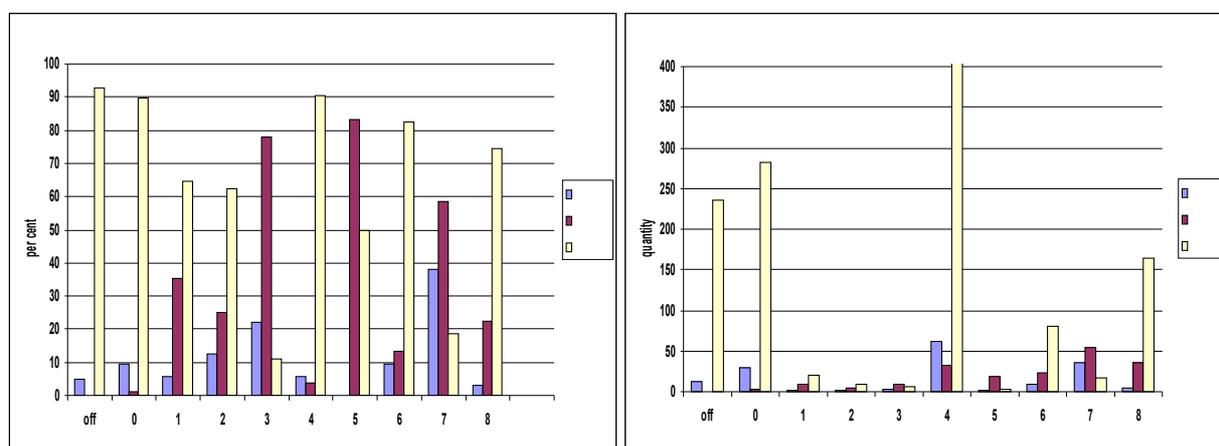


4'7§ comparison of approaching modes between Bocas del Toro and Manzanillo. None of the shown approaching modes differ significantly.

4'6§ Mann-Whitney-U-test: comparison of responses to different approaching modes between areas.

	Mann-Whitney-U = 19315.5 Z = - 0.354 p= 0.723	Mann-Whitney-U = 19468 Z = - 0.000 p= 1.000	Mann-Whitney-U = 19146 Z = - 0.808 p= 0.419
:	Mann-Whitney-U = 5852 Z = - 0.907 p= 0.365	Mann-Whitney-U = 6064.5 Z = - 0.612 p= 0.540	Mann-Whitney-U = 5813 Z = - 1.009 p= 0.313
6	Mann-Whitney-U = 50344 Z = - 1.415 p= 0.157	Mann-Whitney-U = 51028.5 Z = - 1.285 p= 0.199	Mann-Whitney-U = 51837.5 Z = - 0.248 p= 0.805

It was impossible to decide if responses of dolphins to other approaching modes differed between areas or not. In addition circles around dolphin groups (mode 7) were particularly made in Bocas del Toro. So subsequently just data from Bocas del Toro will be discussed.



= 4'1\$ approaching modes – per cent (left) and quantity (right) - in Bocas del Toro. Boats provoked more negative responses if they were fast, directed at the dolphin pod or approaching with changes in speed. Boats with the engine switched off were more likely to be ignored. Vessels which went parallel to the dolphins, with constant slow speed provoked a small percentage of negative reactions. 0 = idle running; 1 = fast, directed at the dolphin pod, changes of speed; 2 = fast, not directed at the dolphin group, no changes of speed; 3 = fast, directed at the dolphin pod, no changes of speed; 4 = slowly, parallel to the dolphin group, no changes of speed; 5 = slowly, persistent in persecuting dolphin groups, changes of speed; 6 = slowly, directed at the dolphin group, no changes of speed; 7 = making circles; 8 = fast, not directed at the dolphin group, no changes of speed.

No negative reaction was observed if the engine was off (Fig. 3.6). If the engine was on, but the boat immobile a few negative responses occurred, but a lot of more positive and neutral responses were found. These two approaching modes differ just in their neutrality (positive: Mann-Whitney-U = 37257,  $Z = -1.908$ ,  $p = 0.056$ , negative: Mann-Whitney-U = 38564,  $Z = -1.542$ ,  $p = 0.123$ , Mann-Whitney-U = 36852,  $Z = -2.343$ ,  $p = 0.019$ ). If the engine is off dolphins are more likely to ignore boats.

All other approaching types are more disturbing ( $\chi^2 = 15.968$ ,  $df = 2$ ,  $p > 0.001$ ).

Boats that were fast, directed at the dolphins without changes of speed, slow boats that were persistent in persecuting dolphin groups or those that made circles around them provoked the highest percentage of negative responses (Fig. 3.6).

But all other fast vessels, with exception of those that approached parallel and without changes in speed (approaching mode 8) did not differ significantly from them ( $\chi^2 = 8.875$ ,  $df = 4$ ,  $p = 0.064$ ).

The responses to boats that approached fast, but not directed to the dolphins and with constant speed did not differ significantly from the responses provoked of slow boats that were directed at the dolphins with constant speed (Mann-Whitney-U = 2285,  $Z = -1.409$ ,  $p = 0.159$ ). But both approaching types provoked more negative reactions than slow approaching parallel to the dolphin group with constant speed (4 to 6: Mann-Whitney = 48830,  $Z = -3.960$ ,  $p = 0.000$ ; 4 to 8: Mann-Whitney-U = 39256.5,  $Z = -7.054$ ,  $p = 0.000$ ).

The only mode of moving that exclusively was performed by whale-watching boats was circulating around dolphin groups. Circles provoked a lot of negative reactions but at the same time the most positive reactions found in this study. Often a part of the group fled, while others stayed and started to leap in the waves, made by the boat.

Generally fast boats, like Local Transport boats, seemed to induce more negative reactions than slow boats (Mann-Whitney-U = 90390,  $Z = -17.743$ ,  $p > 0.001$ ) with one exception if the boat persecuted the dolphin pod. Vessels that were directed at the group, a approaching mode that often was seen in whale-watching boats or the motorized catamaran, produced more negative reactions than those that went parallel to the dolphins (Mann-Whitney-U = 71044,  $Z = -6.358$ ,  $p > 0.001$ ).

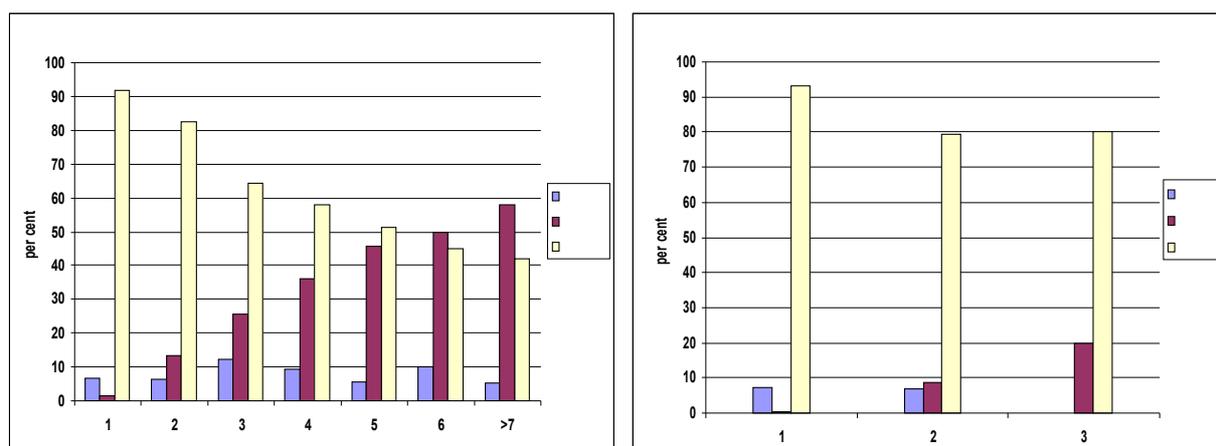
In addition changes in speed seemed to be important (Mann-Whitney-U = 1864,  $Z = -2.454$ ,  $p = 0.014$ ).

So the less intrusive approaching mode is slowly, parallel to the dolphin group with constant speed. Boats interacting with dolphins should perform this approaching mode and stay immobile whenever possible.

## §

In Bocas del Toro the highest number of boats that were present at one time was nine, while in Gandoca-Manzanillo never more than three boats were sighted.

There was a clear increase of negative responses with increasing boat number in both areas (Bocas:  $\chi^2 = 453.232$ ,  $df = 6$ ,  $p > 0.001$ , Manzanillo:  $\chi^2 = 27.813$ ,  $df = 2$ ,  $p > 0.001$ )(Fig. 3.7).



= 48\$ responses to different boat numbers in Bocas del Toro (left) and Gandoca-Manzanillo (right). With increasing boat number the negative effect augmented. In Bocas del Tor the neutrality decreased with increasing boat number.

In Bocas del Toro as negative reactions augmented with increasing boat number, the more the neutral responses decreased ( $\chi^2 = 276.201$ ,  $df = 6$ ,  $p > 0.001$ ). But this tendency was not observed in Gandoca-Manzanillo ( $\chi^2 = 5.492$ ,  $df = 2$ ,  $p = 0.064$ ).

In Manzanillo the augmentation of negative reactions with increasing boat number was slower than in Bocas del Toro. There was a significant difference between negative responses when two boats were present (Mann-Whitney-U = 12854.5,  $Z = -13.072$ ,  $p > 0.001$ ) but there was no difference between the responses to two boats in Bocas del Toro and to three boats in Gandoca-Manzanillo (Mann-Whitney-U = 1324,  $Z = -0.430$ ,  $p = 0.667$ ). Thus, it seems that in Bocas del Toro dolphins are more sensible to number of boats.

So it seems that in the study site in Panama dolphins reacted more sensible to boats.

In Bocas del Toro a significant increase in negative responses as well as a significant decrease in neutral responses was found between one and two (Mann-Whitney-U = 401115,  $Z = -11.513$ ,  $p > 0.001$ ), and two and three boats (Mann-Whitney-U = 53.606,  $Z = -4.291$ ,  $p > 0.001$ ). Between three and four boats no difference was found (Mann-Whitney-U = 11500.5,  $Z = -1.941$ ,  $p = 0.052$ ) but between three and five boats (Mann-Whitney-U = 3095,  $Z = -2.349$ ,  $p = 0.019$ ). From four boats to more than seven boats no significant difference was found ( $\chi^2 = 4.170$ ,  $df = 3$ ,  $p = 0.244$ ). Negative responses of dolphins increased fast to a high level and then slow down. The curve progression looks like a saturation curve.

Hence the saturation of negative responses would be obtained at approximately 60%. With other words dolphins probably would not react more than 60% of the time negative and perform avoidance tactics like fleeing, diving or directional changes. If they were harassed

more by boats (and for a long time) they may show other avoiding strategies like for example avoidance of the area.

So, if they were reacting negative in 30% of the time that they were interacting with boats, this would mean that they show half-maximum negative response.

They would react half as much negative as generally possible.

30% of the reactions are negative if a quantity of three to four boats are present (Fig.3.7).

I propose a maximum of three boats because I think it is better to expose them to a little less stress than the half-maximum level.

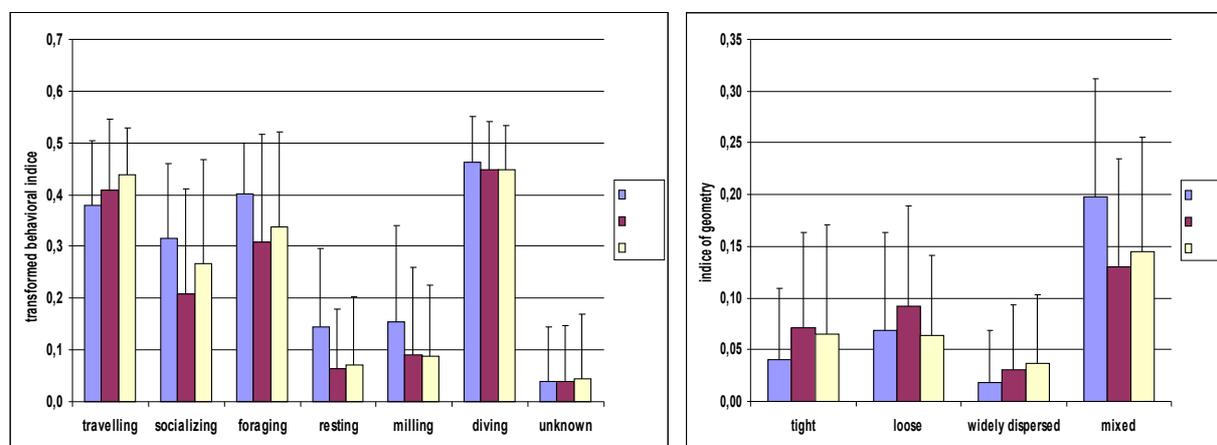
If the whale-watching boats, that mainly interact with dolphins, were using other approaching modes, like that proposed before, four boats may be permitted.

But further investigation is needed to determine the usefulness of this proposal.

## 4'6

There was not a significant variation in the behavior of bottlenose dolphins in the presence of boats ( $p>0.05$ ). However, there seemed to be a tendency to increase travelling and decrease socializing, foraging, resting and milling behavior when boats were present (Fig. 3.8).

Likewise no significant difference in the spaial geometry of the group before, during and after the presence of boats was observed. Although there seemed to be a tendency to less mixed and more tight and loose groups during boats were presence.



= 4'3\$ behavior (left) and group geometry (right) before, during and after interactions with boats. No significant differences were found.

However, when considering only whale-watching boats there were significant differences in travel activities ( $\chi^2 = 6.059$ ,  $df = 2$ ,  $p = 0.048$ ). Dolphins travelled more during and after the interaction with whale-watching boats.

Interactions between dolphins and boats were very low in Gandoca-Manzanillo, data collected by Laura May-Collado can be observed in Table 3.5. However, even these small set of data also suggest that dolphins in Gandoca-Manzanillo are susceptible to whale-watching boats. Four groups out of nine (11 out of 18 interactions) changed their behavior in response to boats. Changes in behavior consisted primarily of changes of their former behavior to travelling.

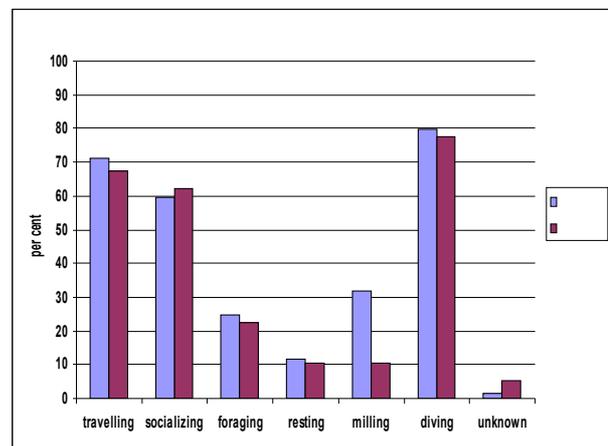
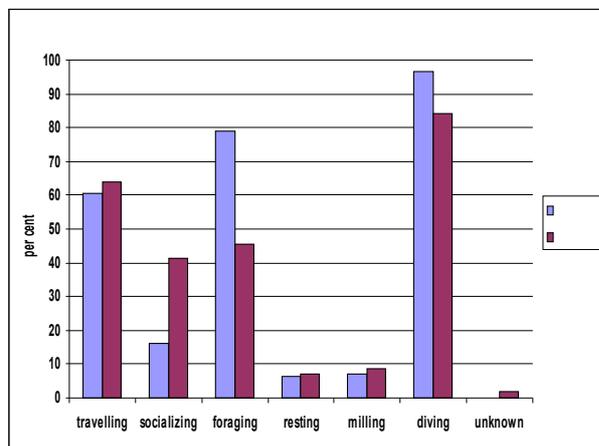
47§ reaction of dolphins to boats in Manzanillo. F = Fishing boats, Js = Jetski, Ps = Personal boats, R = Research boats, WW = Whale Watching boats. Approaching modes: 1 = fast, changes of speed, directed to group, 2 = fast, changes of speed, not directed to group, 3 = fast, no changes of speed, directed to the group, 4 = slowly, no changes of speed, parallel to the group, 5 = slowly, changes of speed, persistent in persecuting the group. (data from L. May-Collado)

							*		
		!	%		+	+	2	"	%
1	Social	Social	Social		x		WW	40	3
	Social	Social	Social	x			WW	?	4
	Social	Social	Social			x	WW	?	4
2	Foraging	Traveling	Traveling				R	115	4
	Foraging	Traveling	Traveling				WW	?	4
	Foraging	Traveling	Traveling		x		Js	?	1
	Foraging	Traveling	Traveling		x		Ps	?	1
3	Social	Traveling	Traveling		x		WW	?	5
	Social	Traveling	Traveling			x	WW	?	4
	Social	Traveling	Traveling			x	WW	?	2
4	Foraging	Foraging	traveling			x	F	50	2
	Foraging	Foraging	traveling			x	WW	50	5
	Foraging	Foraging	traveling			x	F	40	2
5	Foraging	Foraging	Foraging			x	WW	75	4
6	Foraging	Foraging	Foraging			x	WW	75	4
7	Traveling	Traveling/Soc	Traveling	x		x	WW	75	4
8	Social	Traveling	Traveling		x		WW	75	3
9	Traveling	Traveling	Traveling		x	x	WW	75	4

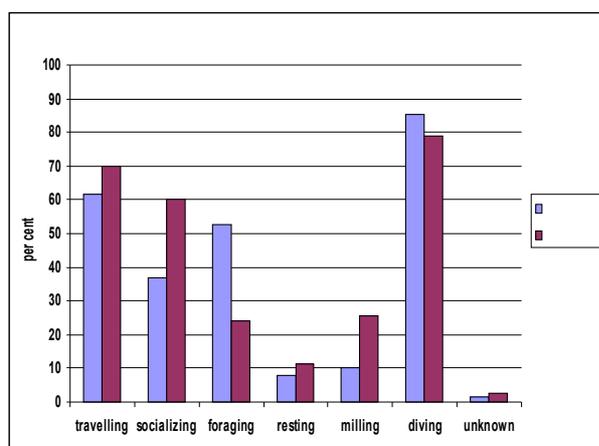
## 4'7 !

There was a significant association between time of the day and dolphin activities. In Bocas del Toro bottlenose dolphins tended to invest more time foraging (Mann-Whitney-U = 11778,  $Z = -6.278$ ,  $p > 0.001$ ) and diving (Mann-Whitney-U = 15514,  $Z = -3.582$ ,  $p > 0.001$ ) in the morning than in the afternoon, meanwhile they socialized more in the afternoon (Mann-Whitney-U = 13276,  $Z = -4.940$ ,  $p = 0.000$ ) (Fig. 3.9).

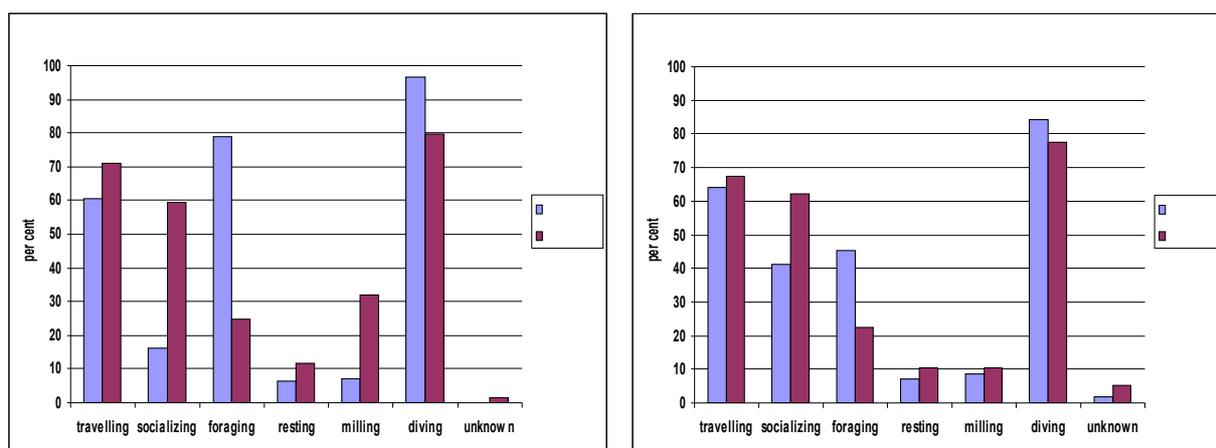
In Gandoca-Manzanillo bottlenose dolphins did not show a significant association between activity and time of the day, except for milling which occurred more often in the morning than in the afternoon (Mann-Whitney-U = 3140,  $Z = -3.149$ ,  $p = 0.002$ ) (Fig. 3.9).



= 4'5\$ diurnal behavior of bottlenose dolphins in Bocas del Toro (left) and Gandoca-Manzanillo (right). In Bocas del Toro a significant difference in socializing, foraging and diving between morning and afternoon was found. In Manzanillo there is a significant difference in milling between morning and afternoon.



= 4'):\$ comparison of whole day behavior of Bocas del Toro and Manzanillo without boats. There is a significant difference in socializing, foraging, milling and diving.



= 4')\$ comparison of morning (left) and afternoon (right) behavior between Bocas del Toro and Manzanillo. There is a significant difference in socializing, foraging, milling and diving in the morning and a significant difference in socializing and foraging in the afternoon.

In Bocas del Toro bottlenose dolphins invested more time foraging (Mann-Whitney-U = 27471,  $Z = -7.310$ ,  $p > 0.001$ ) and diving (Mann-Whitney-U = 36577,  $Z = -2.901$ ,  $p = 0.004$ ), while they invested less time socializing (Mann-Whitney-U = 29514,  $Z = -6.184$ ,  $p > 0.001$ ) and milling (Mann-Whitney-U = 33262,  $Z = -5.733$ ,  $p > 0.001$ ) than in Gandoca-Manzanillo (fig. 3.10).

Although dolphins in Bocas del Toro foraged more in the morning than in the afternoon, they always foraged more than in Gandoca-Manzanillo at arbitrary time of the day (morning: Mann-Whitney-U = 3902,  $Z = -8.775$ ,  $p > 0.001$ ; afternoon: Mann-Whitney-U = 6383,  $Z = -3.242$ ,  $p = 0.001$ ) (Fig. 3.11).

In contrast bottlenose dolphins from Gandoca-Manzanillo invested more time socializing than the dolphins from Bocas del Toro throughout the day (morning: Mann-Whitney-U = 4852,  $Z = -7.162$ ,  $p > 0.001$ ; afternoon: Mann-Whitney-U = 6568,  $Z = -2.902$ ,  $p = 0.004$ ) (Fig. 3.11).

In addition, bottlenose dolphins from Gandoca-Manzanillo appeared to socialize more in mixed groups with the Guyanese dolphin than in single species groups. These results are concordant with those reported by Acevedo-Gutierrez et al. (2005) where social activities were more frequency in mixed-species

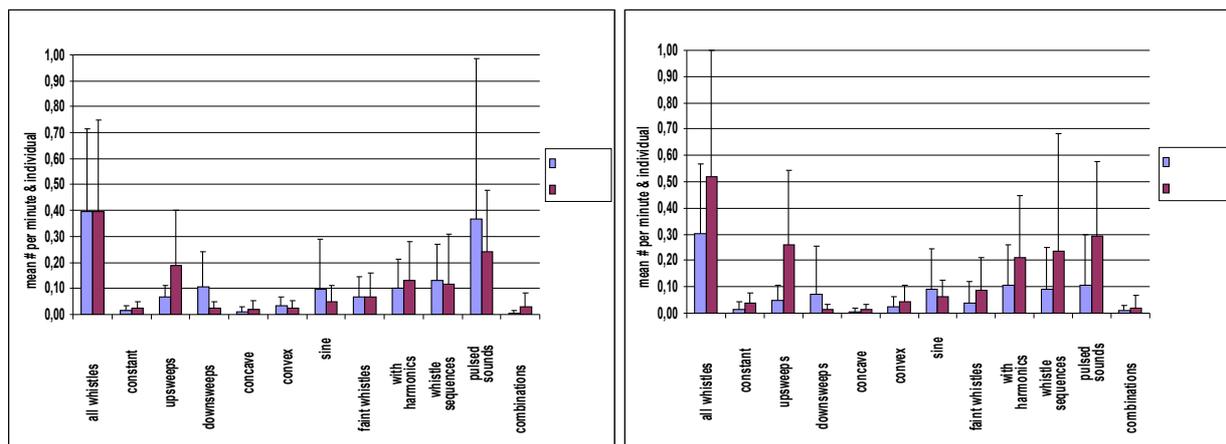
41 9 2 2

There was no significant difference in quantity of sound production between areas or in dependence on boats (Fig. 3.12 a-d). The production rate of pulsed sounds was 0.37 and 0.24 sounds per minute in Bocas del Toro and Gandoca-Manzanillo respectively.

During encounters with boats the rate increased slightly in Bocas del Toro, while it decreased in Gandoca-Manzanillo after boat encounters. But variability of the production rate was always high and no significant variation was found between situations with and without boats.

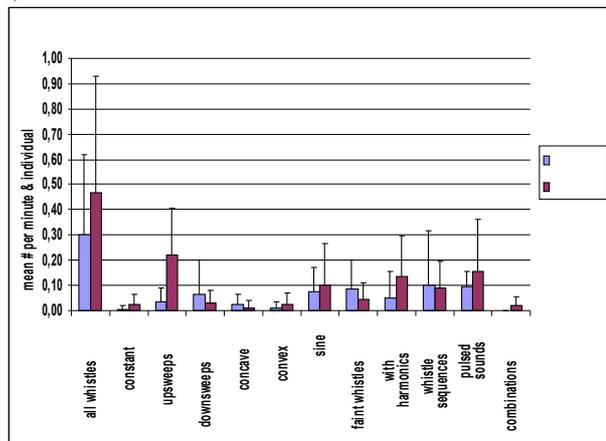
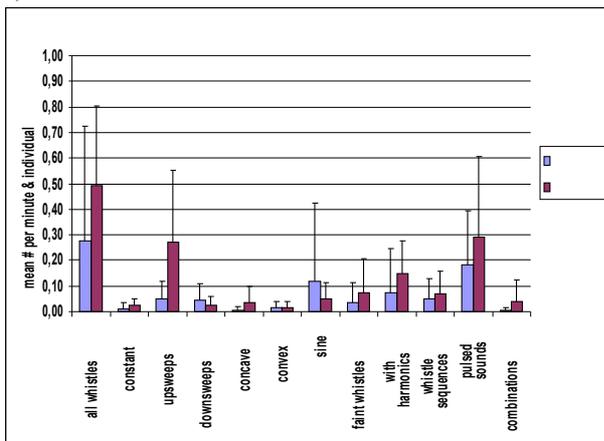
This indicates that factors other than boats (like e.g. behavior) influenced the production rate, or that specific pulsed sound types increased while others decreased.

Combinations of pulsed sounds and whistles were rare in both areas with and without boats.



a)

b)



c)

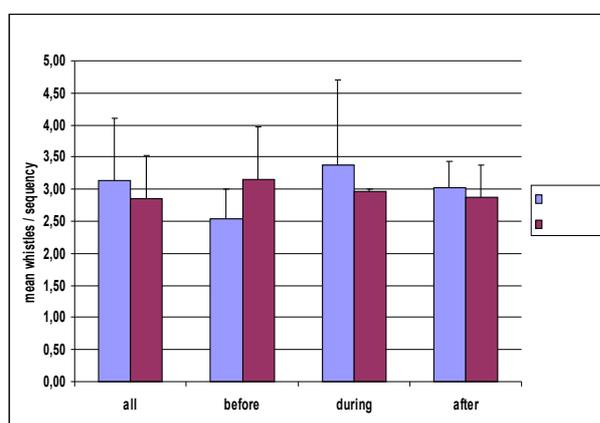
d)

= 4'). \$ mean quantity of sound categories per minute and individual a) all and b) before c) during and d) after the presence of boats. No differences were found between Bocas del Toro and Manzanillo and between pre- during and post-boat situations.

Whistle production rate was 0.40 per minute and individual. In both areas about 25 % of the whistles had harmonics. Harmonic production rates were highest before boat encounters and decreased with boats. But variation in each category (before, during, after) was higher than the variation between categories.

Furthermore there were no significant differences in the production of whistles per whistle sequence between areas or between pre-, during and post-boat situations (Fig. 3.13).

In Bocas del Toro whistles per sequence ranged from two to nine, while they ranged from two to eight in Manzanillo. The mean whistle quantity per whistle sequence was about three in both areas.



= 4) mean quantity of whistles per sequence.  
Comparison between Bocas del Toro and Manzanillo and between situations before, during and after the presence of boats.  
No significant differences were found.

However, the composition of whistle contours was significantly different between areas. In Bocas del Toro the predominant whistle shape was downsweep (34 %), while in Gandoca-Manzanillo upsweeps were the most common (56 %). In Bocas del Toro whistle contour changed considerably with boat presence. Before a boat arrived 45% of all whistles were downsweeps, while the boat was present percentage decreased to 17 %, while 56% of all whistles had sine contour (these whistles are more frequency modulated) and after it was gone the percentage of downsweeps increased to 40 % again (Fig. 3.14).

In Gandoca-Manzanillo upsweeps were always the predominant whistle type, although percentage decreased from 62 % before to 49 % when a boat was present. In the presence of boats whistle production of with other contour types increased similarly. After the boat was gone upsweeps whistles increased to 58 % (Fig. 3.15).

= **4)6§** whistle composition of dolphins in Bocas del Toro. Downsweeps were the most common whistle without boats, while sine whistle were the most produced whistle in the presence of boats. Percentage of whistle shapes: all: 4% constant, 19% upsweep, 34% downsweep, 3% concave, 9% convex, 30% sine; before: 8% constant, 16% upsweep, 45% downsweep, 4% concave, 7% convex, 19% sine; during: 3% constant, 16% upsweep, 17% downsweep, 1% concave, 7% convex, 56% sine; after: 3% constant, 23% upsweep, 40% downsweep, 5% concave, 13% convex, 16% sine

= **4)7§** whistle composition of dolphins in Manzanillo. Upsweeps were the most common whistle with and without boats. Percentage of whistle shapes: all: 8% constant, 56% upsweep, 5% downsweep, 4% concave, 9% convex, 18% sine; before: 6% constant, 62% upsweep, 3% downsweep, 2% concave, 12% convex, 15% sine; during: 8% constant, 49% upsweep, 9% downsweep, 7% concave, 7% convex, 20% sine; after: 9% constant, 58% upsweep, 4% downsweep, 1% concave, 7% convex, 21% sine

4'8 %

28 whistles from Bocas del Toro and 30 whistle from Gandoca-Manzanillo could be analyzed. Descriptive statistics for whistle acoustic parameters are shown in Table 3.6.

4'1\$ range, mean and standard deviation of the ten measured parameters in Bocas del Toro and Gandoca-Manzanillo. Delta, peak, start and end frequencies differed significantly.

				#		
	range	mean	s.d.	range	mean	s.d.
<b>D 2 A0</b>	3.46-15.28	6.70	2.67	1.56-10.88	5.83	2.47
<b>&gt; D 2 A0</b>	9.50-26.64	16.10	4.46	4.79-30.51	18.27	5.93
<b>! D 2 A0</b>	1.34-20.11	9.40	5.27	3.14-22.36	12.44	4.74
<b>A D 2 A0</b>	4.98-19.63	10.14	3.74	3.75-30.38	13.69	6.28
<b>&amp; D 2 A0</b>	4.69-18.46	11.62	3.26	4.13-15.75	8.36	2.91
<b>" D 2 A0</b>	4.39-19.92	9.35	4.34	2.63-29.63	14.06	7.16
<b>!</b>	0.127-3.022	0.945	0.684	0.090-3.020	0.926	0.849
	0.170-14.092	2.813	3.571	0.375-6.338	2.273	1.473
<b>*</b>	0-11	2.14	2.95	0-29	3.67	6.55
<b>0</b>	0-5	1.75	1.65	0-9	2.40	1.81

In Bocas del Toro dolphins lifted maximum ( $\chi^2 = 8.517$ ,  $df = 2$ ,  $p = 0.014$ ) and start frequency ( $\chi^2 = 15.322$ ,  $df = 2$ ,  $p > 0.001$ ) in encounters with boats (Fig.3.16).

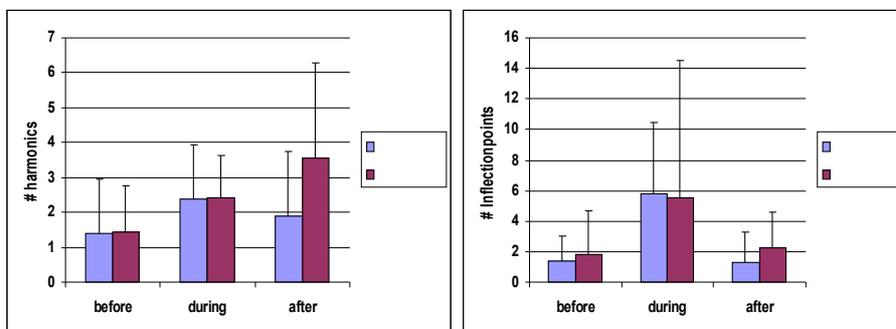
After the boat was gone maximum frequency dropped fast to initial frequency level again (before-after: extremest difference = 0.415, Kolmogorov-Smirnov-Z = 0.988,  $p = 0.284$ ), while the start frequency dropped gradually (before-after: extremest difference = 0.769, Kolmogorov-Smirnov-Z = 1.829,  $p = 0.002$ ).

There were not significant difference in number of harmonics or inflection points (Fig. 3.17), but the highest numbers for inflection points were reached while boats were present.

The standard deviation of minimum, delta, peak and end frequency as well as of duration and modulation increased with boats (Fig. 3.16).

It seems that dolphins adjusted frequencies, duration and modulation inconsistent for these parameters. While some dolphins increased frequencies, modulation or duration during encounters with boats others decreased them. Thus the dispersion increased but the mean value of each parameter remained at the same range.

= 4') 1\$ minimum, maximum, delta, peak, start and end frequency, duration and modulation of whistles in Bocas del Toro before, during and after a boat has been present.



4') 8\$ comparison of number of harmonics and inflection points between Bocas del Toro and Manzanillo before, during and after a boat has been present.

= 4)3\$ minimum, maximum, delta, peak, start and end frequency, duration and modulation of whistles in Manzanillo before, during and after a boat has been present.

In Manzanillo no boat related differences were found (Fig. 3.18).

Minimum, maximum and start frequency increased slightly during the presence of boats, but differences were not significant ( $p > 0.05$ ).

Like in Bocas del Toro modulation and duration showed a greater standard deviation when boats were present.

Whistles with most harmonics were produced after a boat passed away, and whistles had more inflection points in the presence of boats (fig. 3.17), but neither of these results were significantly.

= **4')5§** comparison of all acoustic data between Bocas del Toro (left) and Manzanillo (right). Minimum, maximum, delta, peak, start and end frequency, duration and modulation are illustrated.

In figure 3.19 all whistle data of Gandoca-Manzanillo and Bocas del Toro are shown. Bottlenose dolphins from both localities differ significant in their delta, peak, start and end frequency (delta: extremest difference = 0.410, Kolmogorov-Smirnov-Z = 1.558, p = 0.016, peak: extremest difference = 0.379, Kolmogorov-Smirnov-Z = 1.441, p = 0.031, start: extremest difference = 0.462, Kolmogorov-Smirnov-Z = 1.758, p = 0.004, end: extremest difference = 0.395, Kolmogorov-Smirnov-Z = 1.504, p = 0.022). The differences in end and start frequencies could certainly been explained by the preference of downsweeps and upsweeps in Bocas del Toro and Gandoca-Manzanillo respectively.

No significant difference was found between study sites before a boat arrived (Fig. 3.20).

In Manzanillo minimum, maximum, peak, start and end frequencies expanded over a bigger frequency span, while the standard deviation of duration and especially modulation was greater in Bocas del Toro.

= 4'. :\$ comparison of acoustic data which were recorded before a boat arrived in Bocas del Toro (left) and Manzanillo (right). Minimum, maximum, delta, peak, start and end frequency, duration and modulation are illustrated.

In contrast when a boat was present bottlenose dolphins from Bocas del Toro whistled with significantly higher start frequency (extremest difference = 0.929, Kolmogorov-Smirnov-Z = 1.782,  $p = 0.003$ ). All frequencies, but the end frequency were slightly higher in Bocas del Toro, although differences were not significant (Fig. 3.21). Maximum, delta and peak frequency extended over a bigger frequency range in Bocas del Toro.

In both areas whistle duration varied considerable. Not significant differences were found in whistle modulation. However, there is a trend in bottlenose dolphins from Bocas del Toro to produced more modulated whistles than those produced by bottlenose dolphins from Gandoca-Manzanillo.

4'.) \$ comparison of acoustic data which were recorded while a boat has been present in Bocas del Toro (left) and Manzanillo (right). Minimum, maximum, delta, peak, start and end frequency, duration and modulation are illustrated.

After the boat was gone in Bocas del Toro and Gandoca-Manzanillo, dolphins whistles differ significantly in their maximum frequency (extremest difference = 0.757, Kolmogorov-Smirnov-Z = 1.536,  $p = 0.018$ ) (Fig.3.22). While in Gandoca-Manzanillo maximum frequency slightly increased with boat presence, in Bocas del Toro maximum frequency dropped rapidly to initial frequency level again after the boat was gone. All other parameters do not differ significantly.

4'. . \$ comparison of acoustic data which were recorded after a boat has been present in Bocas del Toro (left) and Manzanillo (right). Minimum, maximum, delta, peak, start and end frequency, duration and modulation are illustrated.

Results from comparison with and without boats show the same pattern than comparison of data before, during and after the presence of boats.

Just in Bocas del Toro more inflection points were found with boats than without boats (Mann-Whitney-U = 24.0, Z = - 2.101, p = 0.036).

But latter is thought to be more precisely because the gradually dropping of start frequency in Bocas del Toro indicates that acoustic alterations of bottlenose dolphins did not stop immediately after the boat has gone.

## 6' !

Both study areas differed considerable in boat traffic and hence in their underwater noise levels. In Bocas del Toro boat traffic was over three times more intensive than in Gandoca-Manzanillo. Motorboats produce a source level that range from 145 to 169 dB re 1  $\mu$ Pa @ 1m increasing with speed and cover a frequency range of 0.1 to 20 kHz (Erbe, 2002). For bottlenose dolphins boat engine are within the range of their optimal audibility, which according to Johnson (1966) is between 15 to 110 kHz at a level around 55 dB re 1 $\mu$ Pa (defined as 10 dB from maximum sensitivity).

Noise from boats was suggested to produce a temporary threshold shift of 5 dB after 30-50 minutes in Killer whales (*Orcinus orca*) (Erbe, 2002). Nachtigall et al. (2004) measured the threshold shift of a bottlenose dolphin after 30 minutes of exposure to noise and found that the highest threshold shift (8 dB) occurred at frequencies between 8 to 16 kHz (maximum 16 kHz) at a source level of 160 dB re 1 $\mu$ Pa. Frequency range and source level matched with the noise produced by the boat engines. Thus engine noise has potential negative effects on dolphin habitats. Long and subsequent interactions with boats may be detrimental for these animals which tend to rely almost exclusively on sound to survive. Sound in dolphins is used to passively and actively search for prey, to keep group cohesion, for mother and calf communication, and to detect predators (Richardson et al. 1995).

In both areas whale-watching boats were found to interact more frequently with the dolphin populations than any other type of boat.

Thus, it is not surprising that in both study areas, whale-watching boats caused more negative reactions than any other type of boat.

However it is noticeable that bottlenose dolphins in Bocas del Toro responded more negative to whale-watching boats than dolphins in Gandoca-Manzanillo.

There are certainly several reasons for this difference.

First the engine power in Gandoca-Manzanillo were found to be preferentially of less than 50 hp. This study showed that significant less negative reactions appear to these small engine types than to other engines with more power.

Similarly results were found by Krieb and Rahadi (2004). During their study on Irrawaddy dolphins (*Orcaella brevirostris*) in Indonesia they noticed that dolphins dove significantly less when boats with engines smaller than 40 hp passed by in contrast to speedboats or container boats. Increased diving times were found in many studies about whale-watching tourism and was interpreted as vertical avoidance tactic which is similar to predator avoiding tactics (Erbe, 2002; Krieb and Rahadi, 2004, Leung Ng and Leung, 2003; Lusseau, 2003, Moore and Clarke, 2002; Nowacek et al., 2001).

In Gandoca-Manzanillo whale-watching possibly move in less harassing ways than in Bocas del Toro, but because of the small sample size this can not be determined.

However, in Gandoca-Manzanillo boats were not found to make circles around dolphin groups like it was often practiced in Bocas del Toro (Fig. 3.6).

Finally the reactions of dolphins depended on the number of boats interacting with them simultaneously. In the study site the highest number of boats interacting with dolphins was nine and three in Bocas del Toro and Gandoca-Manzanillo respectively.

Different reactions depending on the approaching mode were found.

Four groups of approaching modes that are increasingly harassing to dolphins were identified:

1. motionless (either engine off or idle running) (off+mode 0)
2. moving parallel, slowly and with constant speed (mode 4)
3. moving with constant speed either slowly and directed to the dolphin group or fast and parallel (mode 6+8)
4. moving fast directed to the dolphin group, fast and with changes in speed, slowly but persistent in persecuting the dolphin group or making circles around the group (1+2+3+5+7).

Lusseau (2006) assessed that the most important component for interactions with dolphins is the predictability of the vessel. This assumption goes in accordance with the findings of this

study. When boats circled the dolphins probably had difficulties to estimate the exact position of the boat when they are surfacing to breath. Similarly, changes in speed, either moving fast or slow make the prediction of their movement difficult. In fact, many negative responses of dolphins in this study were caused by boats using these types of approaching modes. However, occasionally, circling around the dolphins provoked positive responses, such as jumping in the waves behind boats. Bocas Torito is a land enclosed area where just occasionally wind generated waves occur. Boat generated waves seemed to awake the play instinct of dolphins especially if they were socializing before boat interaction started. But negative responses to circles were clearly more frequently than positive responses. Thus this kind of approaching mode should be restricted in the future.

Not only the predictability seemed to be important but also the level of obtrusion.

So boats that persecuted the dolphins with constant speed and constant distance and fast moving boats that approached parallel to the dolphin group are both moving in a predictable way. Nevertheless they provoked more negative responses of dolphins than slowly parallel approaching boats.

In Bocas del Toro the motorized catamaran and boats for local transport were found to provoke as much negative responses of dolphins than whale-watching boats. This may be due to the approaching modes of these type of boats.

The catamaran often was found very near to the dolphin group, persecuting it with constant speed, while boats of Local transport always passed in high speed, sometimes directed to the dolphin group.

Nowacek (2001) studied the behavior of bottlenose dolphins in interactions with whale-watching boats and found that the distance of boats to the dolphin group was very important. In future work time, distance and arrangement of the boats should be determined additionally to the analyzed approaching modes to increase knowledge of dolphins' reaction.

Dolphins did not react to every type of boat but they were more likely to increase travelling during and after interactions with whale-watching boats. Similar responses to whale-watching boats have been reported in bottlenose dolphins from New Zealand (Lusseau, 2004; Lusseau, 2006). Lusseau (2004) and Ribeiro et al. (2005) suggested that some behavioral states, like milling or feeding are more likely to be disrupted by interactions with boats than others. Milling and resting occurred rarely in Bocas del Toro. To determine if these behavioral categories are susceptible to boats a higher sample size is needed. Additionally some responses may be difficult to detect but may still be of significance to the dolphins (Shane, 1990).

Although not significant, there was a trend in reducing foraging activities in the presence of boats. Because foraging occurs underwater, I do not have information on how boat presence affected foraging success. Potentially, masked echolocation signals (Au, 2000) and avoidance of boats by fishes (Engas et al. 1995) lead to decreased hunting effort.

Thus, animals perhaps decrease foraging and switch to other behavior during the presence of boats because of their decreased foraging effort.

Bottlenose dolphins in Bocas del Toro were found to spend significant more time in foraging than the bottlenose dolphin in Gandoca-Manzanillo if boats were absent. Thus, possibly the dolphins had to compensate the time and energy they lost during encounters with boats.

In further study an underwater camera should be utilized to determine dolphin behavior with more certainty.

In terms of the geometry of the group, boat interaction did not seem to influence group geometry. Concordantly Mattson et al. (2005) and Ribeiro et al. (2005) found that the group geometry seemed to depend more on general behavior than on the presence of boats. For instance, in other populations of bottlenose dolphins, individuals tended to be tight formation when travelling or socializing and more loose, widely dispersed or mixed when feeding (Azevedo et al. 2005; Shane, 1990).

" ! !

Contrary to my previous expectations no changes in sound production of any of the analyzed sound categories occurred during or after interactions with boats. In a prior study of humpback dolphins production of pulsed sounds was not affected by boat presence (Van Parijs and Corkeron, 2001).

In addition, humpback dolphins during and after boat encounters increased their whistle rate to promote group cohesion. However, the studied bottlenose dolphins did not produce significantly more whistles or decrease inter-animal distance in the presence of boats. These dolphins may have developed another strategy to avoid boats. Because tight groups are more likely to be seen by boat operators they may tend to form mixed groups. This happened several times in interactions with a high quantity of boats. In addition, because Bocas Torito is a relatively small area, dolphins can be separated and still be in acoustic contact with each other, since their whistles can propagate over several kilometers (Janik, 2000).

Alternatively they may produce a higher whistle rate just on onset of the boat noise. Lesage et al. (1999) found a higher whistle production rate in the first 1-2 minutes after the onset of noise. Then the production rate decreased when boats moved closer to the whales.

Likewise Buckstaff (2004) found a higher whistle production rate, especially at the onset of approaches in bottlenose dolphins.

Like I determined the production rate during the whole time a boat has been present, such an effect could be undetected.

There was a slightly, but not significant increase toward tighter and looser formation in the Bocas del Toro study site, where geometry has been proved. That could be initiated by a higher whistle production rate and hence support this hypothesis.

The dolphins of Bocas del Toro may use both strategies in dependance on the intensity of boat traffic. Potentially preferring the former strategy if more boats are present.

Further studies are needed to support one of the two or both strategies in Bocas del Toro.

Differences in acoustic behavior of bottlenose dolphins in Bocas del Toro and Gandoca-Manzanillo had been expected due to the distinct level of boat traffic in these areas. Overall, whistles of bottlenose dolphins in this study ranged from about 2 to 30 kHz.

There is no information available on boat engine source levels yet for these areas, thus it is not clear if signals are being masked. However, if engine noise characteristics are similar to those reported by Erbe (2002) the noise level would require adaptations of dolphins.

A shift of whistle frequency to higher values, longer whistle duration and less modulation was expected to be found in Bocas del Toro in comparison to Gandoca-Manzanillo.

These changes were expected based on changes documented on other dolphin populations (Au et al., 1985; Buckstaff, 2004; Lesage et al. 1999).

There were no significant differences in whistle duration or modulation between sites. But some whistle frequency parameters did vary between areas. When comparing the whole data set, bottlenose dolphins from Gandoca-Manzanillo produced whistles with higher end, peak and delta frequency and lower start frequency. These differences may be due to intraspecific variation more than to boat traffic. Downsweep whistles predominated in Bocas del Toro and upsweeps in Gandoca-Manzanillo. Frequency range have been found to differ in several populations of the same odontocete species (Rendell, 1999), but the higher peak frequency in Gandoca-Manzanillo was unexpected as higher frequencies were found to be representative for areas with higher ambient noise level (e.g., Ansmann and Evans, 2006, Au, 1985).

Nevertheless it is doubtful if the comparison of the whole data set does have high expressiveness because there was not found any difference between the whistles in the two study sites if no boats were present.

I analyzed different quantities of whistles in each case before, during and after boat interactions in Bocas del Toro and Gandoca-Manzanillo respectively. This might have produced the differences in frequency parameters of the whole data set.

In Bocas del Toro variation of whistle parameters were found during interactions with boats. A temporary frequency shift occurred in start and maximum frequency, when boats entered the habitat of bottlenose dolphins. Whereas just in Bocas del Toro this shift obtained a significant

value.

There are some evidence that dolphin in louder habitats change their whistle repertoire permanently to higher frequencies (e.g. Ansmann and Evans, 2006). While a temporary shift was reported from some acoustical studies with boat traffic (Buckstaff, 2004; Lesage et al. 1999).

This raise the question which factors are responsible for the advantage of frequency regulation instead of permanent frequency changes.

Au et al (1985) postulated that a dolphin transported to an area with higher ambient noise generated high frequencies as a by-product of producing high intensity clicks. In other words, dolphins can only emit high intensity sounds if they use high frequencies, whereas lower frequencies are always emitted with low intensity. Verfuss (1996) supported this hypothesis for the echolocation behavior of a river dolphin.

Moreover, Lesage et al. (1999) investigated the effect of boat noise on the vocal behavior of belugas. Belugas shifted the mean frequency of their whistles during the presence of motorboats, but this shift was not strong enough to avoid the noisy frequency band of the boats. Lesage et al. (1999) suspected that analogue to the frequency shift in echolocation clicks, whistle frequency may be arised in order to increase source level.

Increase in dominant frequency as by-product of high amplitude sounds has also been observed in mating white-lipped frogs (Lopez et al. 1988) and may be a general occurrence.

But louder sounds may be associated with energetic loss (Cynx et al., 1998).

Most whale-watching boats in Bocas del Toro arrived in the morning, while less boats were sighted in the afternoon.

In an area with changing boat traffic and hence background noise, modulation of frequency instead of permanent alteration might be in order to save energy.

Otherwise the reduction of frequency after boats passed by could also happen in order to communicate over wide distances like proposed by Morisaka et al. (2005).

During boat encounters in Bocas del Toro sine whistles were predominant, not downsweep whistles (see pie chart Figures 3.14). Sine whistles are the most frequency modulated whistle contour. As mentioned before, frequency increase of inflection points are another way to contra

rest high levels of noise. The shift to sine whistles in Bocas del Toro may happen in order to increase the variability of whistle frequency. Like changes in general provoke more attention in the recipient, this could be an advantage in situations with high noise level (Ding et al. 1995).

A shift from a dominant contour shape to another during exposure to boat noise was also found for belugas (Lesage et al., 1999). Belugas shifted their predominant constant whistles to downsweeps during noise exposure. Both structures are simple in shape. Nevertheless they changed their simpler whistle contour to a complexer one.

Bottlenose dolphins from Gandoca-Manzanillo emitted mainly upsweeps whistles and no changes in whistle contour occurred during or after encounters with boats. Because of the shift from simple whistle contours to more complex ones (sine whistles) in Bocas del Toro, it appears that Bocas bottlenose dolphins reacted more sensible to boat presence than those from Gandoca-Manzanillo.

Alternatively upsweeps are more suited for background noise making a change to other whistle shapes unnecessary.

Upsweeps are simple in structure given their lack in amplitude modulation and are highly transmissible (Richards, 1981).

In Gandoca-Manzanillo *Tursiops truncatus* share its habitat with the Guyanese dolphin, *Sotalia guianensis*. Tucuxis (*Sotalia fluviatilis*) and Guyanese dolphins were found to produce upsweep whistles as their predominant whistle contour in many areas (Azevedo and Van Suys, 2005; Erber and Simão, 2004; Rossi-Santos and Podos, 2006).

Similarly, the Guyanese dolphins produce mainly ascending whistles in this study area, although their whistles were not quantified in detail.

Bottlenose dolphins from Gandoca-Manzanillo, where found mostly in mixed-species groups, and thus most of the selected whistles come from these groups. Bottlenose dolphins might be producing mostly upsweeps as their predominant whistle when interacting with the Guyanese dolphin by imitating their predominant whistle contour, like bottlenose dolphins were found to imitate whistles and whistle like sound in many occasions (Fripp et al. 2005, Miksis et al. 2002, Tyack, 1986).

However, it is important to note that I selected whistles from these mixed-species groups based on whistles characteristic obtained from a few single-species groups of bottlenose dolphins. Therefore, it may be that some of the selected whistles were actually emitted by the Guyanese

dolphins and not bottlenose dolphins, and thus I am over representing the upsweep contour whistles. This sampling technique was used because the recording equipment used a single omni-directional hydrophone which does not allow the identification of the whistling individual.

Rendell et al. (1999) suggested that variables with high intraspecific coefficients of variation may be used to communicate information about individuals or groups, such as identity or emotional state. Accordingly, Janik et al. (1994) found varying frequency characteristics in whistles of a bottlenose dolphin depending on the behavioral context and emotional state.

This is interesting as bottlenose dolphins from Gandoca-Manzanillo tend to invest more time in social activities than those from Bocas del Toro. Social activities included aggressive interactions, aerial behavior associated with “play”, mother-calf interactions, and sexual behavior. These highly diverse interactions between animals certainly represent different emotional states and could explain largely the variation observed on the frequency parameters of the bottlenose dolphins from Gandoca-Manzanillo when boats were not present.

During boat interactions bottlenose dolphins from Gandoca-Manzanillo did not show any acoustic reaction to the boats. However, it needs to be clarified that sample size from this study site was very low. Because animals spend more time socializing and in tight spatial formation it is possible that they were less susceptible to boat intrusion (Kreb and Rahadi, 2004; Shane, 1990). This was not the case in Bocas del Toro, where bottlenose dolphin whistle frequency parameters showed an increase in their standard deviation when boats were present. Although changes may be due to different emotional states of individual dolphins, the interaction with the whale-watching boats may as well represent another emotional state.

Lesage et al. (1999) found belugas (*Delphinapterus leucas*) to produce longer whistles and less modulation when interacting with boats.

Longer whistles were explained to be more likely to be heard by conspecifics during interactions with boats.

Indeed in both areas longest whistles as well as highest modulation and highest number of inflection points occurred during encounters with boats. But in contrast in Bocas del Toro also the shortest whistles appeared, while in Gandoca-Manzanillo whistles with lowest coefficient of modulation were found with boats.

In both areas whistles without inflection points were found in either case.

This indicates the great variation between particular whistles in the same context, if no false conclusion was taken due to small sample size.

Caldwell et al. (1990) have studied 22 278 whistles of 126 captive dolphins in four age classes and postulated that different individuals do not always show similar patterns of variations in whistles in the same situation. They found some dolphins that increased and others that decreased number of inflection points or whistle duration with stress.

As exposure to noise is a stressful situation the lack of significant differences could also be an expression of individual and convers stress reactions.

On the other hand this conclusion is arguable as shorter whistles are more likely to be masked by engine noise.

The short-term acoustical and behavioral reactions to engine noise that were found may have accumulative detrimental effects on the bottlenose dolphins of particularly Bocas del Toro where boat traffic is more intense and whale-watching operators more aggressive in their approach to dolphins. Information about engine noise as a cause for permanent threshold shift or hearing loss is not yet available in cetaceans (Erbe, 2002). But long-term changes in the behavioral budget would influence energy budget and reproduction effort (Kreb and Rahadi, 2004; Lusseau, 2004). In addition, dolphins may start avoiding areas as a result of habitat destruction (Lusseau, 2004). Although the local people of Bocas del Toro tells that more dolphins were observed in Bocas Torito a decade ago, dolphins still seem to rely on the area for basic activities such as feeding and socializing. Thus the creation of strategies to regulate the negative effects of noise on these animals is needed.

## 7'

1. The boat traffic in Bocas del Toro was found to be three times more intensive than in Gandoca-Manzanillo. While in Gandoca-Manzanillo just slightly more boats were found in the morning, in Bocas del Toro three times more boats interact with dolphins in the morning than in the afternoon. In the afternoon more boats were found in Gandoca-Manzanillo than in Bocas del Toro.
2. Whale-watching boats interacted more than any other type of boat with dolphins in both areas. Transiting boats normally passed by fast or slowly, with constant velocity, normally parallel to the dolphins but sometimes directed to them. All other approaching types (fast or slowly with changing velocity, circles, persecution) were predominantly shown by whale-watching boats.
3. The approaching mode seems to be more important than engine power and so regulation is necessary.
4. Security and predictability seem to be the key-factors for dolphins in boat approaches. Dolphins showed little negative reactions to boats if the engine was off or idle running, whereas these modes differed only in their neutrality.  
A fast moving boat always generated negative responses of the dolphins. Approaching the group slowly and parallel without changes in speed was found to be the best approaching mode. Fast boats or boats that persecuted dolphins provoked the most negative responses.  
A clear increment of negative responses was found with increasing boat number.
5. Local transport boats in Bocas del Toro and Fishing boats in Gandoca-Manzanillo disturb dolphins as much as whale-watching boats.  
But since whale-watching boats interacted more frequently with dolphins than any other boat type they are of special importance.
6. In Gandoca-Manzanillo dolphin-boat interactions were rare and so it was not possible to

prove if dolphins change their behavior in the presence of boats.

7. In Bocas del Toro dolphins did not change behavior in interactions with boats in general, just in encounters with whale-watching boats they were found to travel more during and after encounters.
8. Dolphins in both areas were not found to change the production of any sound type during or after the encounters with boats.
9. But an influence of the different level of anthropogenic noise was found in the structure of whistles.

In Bocas a shift from downsweep whistles to sine whistles occurred during encounters with boats probably indicating an increase in modulation.

Although no difference in the coefficient of whistle modulation according to Mccowan and Reiss (1995) was found.

In Gandoca-Manzanillo upweeps were the predominant contour in any situation. Potentially because the dolphins were not or less disturbed.

10. Start and maximum frequency of whistles increased with boats presence in Bocas del Toro, but no variations were found in Gandoca-Manzanillo.

---

§

1. So Vessels interacting with dolphins should not exceed three contemporaneously. If appropriate approaching modes, that cause less disturbance are used four boats might be admitted (see recommendation 2.).
2. Since approaching mode was key in dolphin reactions. It is recommend to use the approaching mode in which boats followed dolphins positioning their boat parallel to the dolphin group and keeping the same speed as the dolphins. If dolphins are spending time in a particular area, it is recommended to turn off the engine or to keep the boat immobile. Transiting boats are recommended to reduce speed while passing by a dolphin group especially in Bocas Torito.

3. Whale-watching boats in Bocas del Toro normally arrived in the morning when dolphins were feeding and disturb them in their natural behavior. It would be a good alternativ for boat operators to arrive in the afternoon, when dolphins are socializing.

## 1' % A

My special thank goes to Laura May-Collado, who made this work possible. Thank you for all the good advices you gave to me during this work.

Prof. Dr. Graf, I would like to thank you for the acceptance of this study and for your confidence.

Thank you to all the skippers who conducted the surveys with me, my special thank goes to Eric Brown, who taught me boat driving, to Milton, who told me all these wonderful stories about the indigenous people of Bocas del Toro and to Bacalao and Alfonso – thank you.

Thank you to the team of the Smithsonian Tropical Research Institut, I really enjoyed staying with you. My special thanks go to Gabriel, Plinio, Murray and Urania, who helped me a lot during my stay.

Thank you very much, José David Palacio for the introduction in the field work.

I like to thank my family and my friends, especially Michael Krauß, Bea und Martin Fiutak and Stefan Strauch for all the useful advices and help.

Thank you to Cesar Orlando Carvajal Pereira for believing in me and the good advices, especially during the “hard times“ of this investigation.

Thank you to the DAAD (Deutscher Akademischer Austausch Dienst) for the financial aid. Especially to Mrs. Guzmán for the handling.

Thank you to the Marine Mammal Lab. Florida International University, especially Douglas Wartzok for the acoustical data supply and the permission to use RAVEN.

## 8'

- Altmann, J. (1974) Observational Study of behavior: sampling methods. *Behavior* 49: 227-267
- Ansmann, I.C., Evans, P.G.H. (2006) The whistle repertoire of short-beaked common dolphins, *Delphinus delphis*, around the British Isles. 20<sup>th</sup> Annual Conference of European Cetacean Society, Gdynia, Polonia
- Au, W.W.L., Carder, D.A., Penner, R.H., Scronce, B.L. (1985) Demonstration of adaptation in beluga whale echolocation signals. *Journal of the Acoustic Society America* 77 (2): 726-730
- Au, W.W.L. (2000) Echolocation in Dolphins. In *Hearing by Whales and Dolphins*. eds. Au, W.W.L., Popper, A.N., Fay, R.R. Springer-Verlag New York. pp. 364-408
- Acevedo-Gutiérrez, A., DiBerardinis, A., Larkin, S., Larkin, K., Forestell, P. (2005) Social interactions between Tucuxis and Bottlenose Dolphins, in Gandoca-Manzanillo, Costa Rica. *LAJAM* 4 (1) 49-54
- Azevedo, A.F., Van Suys, M. (2005) Whistles of tucuxi dolphins (*Sotalia fluviatilis*) in Brazil. Comparison among populations. *Journal of Acoustical Society of America* 117 (3): 1456-1464
- Bazúa-Duran, C., Au, W.W.L. (2002) The whistles of Hawaiiin spinner dolphins. *Journal of the Acoustic Society America* 112 (6): 3064-3072
- Blomqvist, C., Amudin, M. (2004) High-Frequency Burst-Pulse Sounds in Agonistic/Aggressive Interactions in Bottlenose Dolphins, *Tursiops truncatus*. In *Echolocation in Bats and Dolphins*. eds. Moss, C.F., Thomas, J.A., Vater, M. The University of Chicago Press, Chicago. pp 425-431
- Buckstaff, K.C. (2004) Effects of watercraft noise on the acoustic behaviour of Bottlenose Dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 20 (4): 709-725
- Boisseau, O. (2005) Quantifying the acoustic repertoire of a population: The vocalization of free-ranging bottlenose dolphins in Fiordland, New Zealand. *Journal of the Acoustic Society America* 117 (4): 2318-2329

- Caldwell, M.C., Caldwell, D.K., Tyack, P.L. (1990) Review of the Signature-whistle Hypothesis for the Atlantic Bottlenose Dolphin. In *The Bottlenose Dolphin*. eds. Leatherwood, S., Reeves, R.R. Academic Press, Inc. San Diego, California. pp. 199-234
- Carillo, M., Tejedor, M. (2006) Marine traffic and the Conservation of Sperm Whale *Physeter Macrocephalus* populations in Canary Islands. Cetacean stranded canarian net 1980-2004. 20<sup>th</sup> Annual Conference of European Cetacean Society, Gdynia, Polonia
- Cranford, T.W. (2000) In Search of Impulse Sound Sources in Odontocetes. In *Hearing by Whales and Dolphins*. Ed. Au, W.W.L., Popper, A.N., Fay, R.R. Springer-Verlag New York. pp. 109-155
- Cubero Pardo, P. (1998) Distribución y patrones de actividad del bufeo (*Tursiops truncatus*) y el delfín manchado (*Stenella attenuata*) en el Golfo Dulce, en relación con variables ambientales. Master thesis at the University of Costa Rica
- Cynx, J., Lewis, R., Tavel, B., Tse, H. (1998) Amplitude regulation of vocalization in noise by a songbird, *Taeniopygia guttata*. *Animal Behaviour* 56: 107-113
- Ding, W., Würsig, B., Evans, W.E. (1995) Whistles of bottlenose dolphins: comparisons among population. *Aquatic Mammals* 21 (1): 65-77
- Durden, W.N. (2005) The harmful effects of inadvertently Conditioning a Wild Bottlenose Dolphin (*Tursiops truncatus*) to Interact with Fishing Vessels in the Indian River Lagoon, Florida, USA. *Aquatic Mammals* 31 (4): 413-419
- Engas, A., Misund, O.A., Soldal, A.V., Horvei, B., Solstad, A. (1995) Reactions of penned herring and cod to playback of original, frequency-filtered and time-smoothed vessel sound. *Fisheries Research* 22: 243-254
- 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(2): 394-418.
- Erber, C., Simão, S.M. (2004) Analysis of whistles produced by Tucuxi Dolphin *Sotalia fluviatilis* from Sepetiba Bay, Brazil. *Anais da Academia Brasileira de Ciências* 76 (2): 381-385

- Evans, P.G.H. (2006) Marine mammals in the european costal zone: past, present and future. 20<sup>th</sup> Annual Conference of European Cetacean Society, Gdynia, Polonia
- Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., Wells, R., Tyack, P. (2005) Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on signature whistles of community members. *Animal Cognition* 8: 17-26
- Gannon, D.P., Barros, N.B., Nowacek, D.P., Read, A.J., Waples, D.M., Wells, R.S. (2005) Prey detection by bottlenose dolphins, *Tursiops truncatus*: an experimental test of the passive listening hypothesis. *Animal Behaviour* 69: 709-720
- Guzmán, H.M., Barnes, P.A.G., Lovelock, C.E., Feller, I.C. (2005) A Site Description of the CARICOMP Mangrove, Seagrass and Coral Reef Sites in Bocas del Toro, Panama. *Caribbean Journal of Science* 41 (3): 430-440
- Hastie, G.D., Wilson, B., Tufft, L.H., Thompson, P.M. (2003) Bottlenose Dolphins increase synchrony in response to boat traffic. *Marine Mammal Science* 19 (1): 74-84
- Hermann, L.M., Tavolga, W.N. (1980) The communication system of cetaceans. In Hermann, L.M. (ed.) *Cetacean Behavior: Mechanisms and Functions*. New York: John Wiley & Sons, pp. 149-211
- Herrera, W. (1985) *Clima de Costa Rica*. Editorial of the Universidad Estatal a Distancia (UNED). San José, Costa Rica
- Herzig, D.L. (1996) Vocalization and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins *Tursiops truncatus*. *Aquatic Mammals* 22 (2): 61-79
- Hoyt, E. (2001) *Whale Watching 2001: Worldwide tourism numbers, expeditures and expanding socioeconomic benefits*. Report from the International Fund for Animal Welfare (IFAW)
- Hoyt, E., Hvenegaard, G.T. (2002) A review of whale-watching and whaling with applications for the Caribbean. *Costal Management* 30: 381-399

- Huggenberger, S., Benke, H. (2004) *Tursiops truncatus*. In Das europäische Schutzgebietsystem Natura 2000 – Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland. Ed. Peterson, B., Ellwanger, G., Bless, R., Boye, P., Schröder, G., Ssymank, A. Bonn Bundesamt für Naturschutz: Schriftreihe für Landschaftspflege und Naturschutz 69 (2): 621-624
- Janik, V.M., Dehnhardt, G., Todt, D. (1994) Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 35: 243-248
- Janik, V.M., Thompson, P.M. (1996) Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine Mammal Science 12: 597-602
- Janik, V.M. (2000) Source Level and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. Journal of Comparative Physiology 186: 673-680
- Johnson, C.S. (1966) Auditory thresholds of the bottlenosed porpoise (*Tursiops truncatus* Montague). U S Naval Ordnance Test Station (NOTS) TP 4178. In Hearing by Whales and Dolphins. Ed. Au, W.W.L., Popper, A.N., Fay, R.R. Springer-Verlag New York
- Johnston, D.W. (2002) The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. Biological Conservation 108: 113-118
- Kammigan, I.C., Bräger, S., Hennig, V., Höschle, C., Pretzlaff, I. (2006) Bottlenose Dolphins (*Tursiops truncatus*) in the Kornati National Park, Croatia: “The tourist season begins – we leave”. 20<sup>th</sup> Annual Conference of European Cetacean Society, Gdynia, Polonia
- Kilian, A. (1993). Untersuchungen zur akustischen Kommunikation bei *Sotalia fluviatilis* Gervais (Delphinidae, Mammalia). Diplom thesis at the Rheinischen Friedrich-Wilhelms university of Bonn, Germany
- Koschinski, S., Culik, B. M., Damsgaard Henriksen, O., Tregenza, N., Ellis, G., Jansen, C. and Kathe, G. (2003) Behavioral reactions of free-ranging porpoises and seals on the noise of a simulated 2MW windpower generator. Marine Ecology Progress Series 265: 263-273.

- Kovacic, I., Bogdanovic, I. (2006) Diet of the Bottlenose Dolphin (*Tursiops truncatus*, Montague 1821) in the Adriatic Sea. 20<sup>th</sup> Annual Conference of European Cetacean Society, Gdynia, Polonia
- Kreb, D., Rahadi, K.D. (2004) Living Under an Aquatic Freeway: Effects of Boats on Irrawaddy Dolphins (*Orcaella brevirostris*) in a Coastal and Riverine Environment in Indonesia. *Aquatic Mammals* 30 (3): 363-375
- Lesage, V., Barrette, C., Kingsley, M.C.S., Sjare, B. (1999) The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. *Marine Mammal Science* 15 (1): 65-84
- Leung Ng, S., Leung, S. (2003) Behavioral response of Indo-Pacific humpback dolphin (*Sousa chinensis*) to vessel traffic. *Marine Environmental Research* doi:10.1016/S0141-1136(03)00041-2  
[online] URL: <http://www.elsevier.com/locate/marenvrev>
- Lopez, P.T., Narins, P.M., Lewis, E.R., Moore, S.W. (1988) Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behaviour* 36: 1295 - 1308
- Lusseau, D. (2003) 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* Vol. 257: 267-274.
- Lusseau, D., Newman, M.E.J. (2004) Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of Biological Sciences (Suppl.)* 271: 477-481
- Lusseau, D., Wilson, B., Hammond, P.S., Grellier, K., Durban, J.W., Parson, K.M., Barton, T.R., Thompson, P.M. (2005) Quantifying the influence of sociality on population structure in bottlenose dolphin. *Journal of Animal Ecology*  
doi: 1111/j.1365-2656.2005.01013.x
- Lusseau, D. (2006) The short-term behavioral reactions of Bottlenose Dolphins to interactions with boats in Doubtful Sound, New Zealand. *Marine Mammal Science*: doi: 10.1111/j.1748-7692.2006.00052.x

- Mattson, M.C., Thomas, J.A., St. Aubin, D. (2005) Effect of boat activity on the behavior of Bottlenose Dolphins (*Tursiops truncatus*) in Waters surrounding Hilton Head Island, South Carolina. *Aquatic Mammals* 31 (1): 133-140
- May-Collado, L., Morales Ramírez, A. (2005) Precencia y patrones de comportamiento del delfin manchado costero, *Stenella attenuata* (Cetacea: Delphinidae) en Golfo de Papagayo, Costa Rica. *Revista de Biología Tropical* 53 (1-2): 265-276
- May-Collado, L.J., Wartzok, D. (2007) The freshwater dolphin *Inia geoffrensis* produces high frequency whistles. *Journal of the Acoustical Society of America* 121(2): in press.
- McCowan, B., Reiss, D. (1995) Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): role of learning. *Journal of Comparative Psychology* 109: 242-260
- Miksis, J.L., Tyack, P.L., Buck, J.R. (2002) Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *Journal of the Acoustical Society of America* 112 (2): 728-739
- Moore, S.E., Clarke, J.T. (2002) Potential impact of offshore human activities on gray whales (*Eschrichtius robustus*). *Journal of Cetacean Research and Management* 4 (1): 19-25
- Morisaka, T., Shinohara, M., Nakahara, F., Akamatsu, T. (2005) Effects of ambient noise on the whistles of Indo-Pacific Bottlenose Dolphin populations. *Journal of Mammalogy* 86 (3): 541-546
- Nachtigall, P.E., Supin, A.Y., Pawloski, J., Au, W.W.L. (2004) Temporary threshold shifts after noise exposure in the bottlenose dolphin (*Tursiops truncatus*) measured using evoked auditory potentials. *Marine Mammal Science* 20 (4): 673-687
- Nowacek, S. M, Wells, R. S. and Solow, A. R. (2001) Short-term effects of boat traffic on the Bottlenose Dolphin, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17(4):673-688
- Olesiuk, P. F., Nichol, L. M. and Ford, J. K. B. (2002) Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoise (*Phocoena, phocoena*) in retreat passage, British Columbia. *Marine Mammal Science* 18(4):843-862

- Rendell, L.E., Gordon, J.C.D. (1999) Vocal response of Long-finned pilot whales (*Globzcephala melas*) to military sonar in the Ligurian Sea. *Marine Mammal Science* 15 (1): 198-204
- Rendell, L.E., Matthews, J.N., Gill, A., Gordon, J.C.D., Macdonald, D.W. (1999) Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *Journal of Zoological Society of London* 249: 403-410
- Ribeiro, S., Vidali, F.A., Freitas, T.R.O. (2005) Behavioural Responses of Chilean Dolphins (*Cephalorhynchus eutropia*) to Boats in Yaldad Bay, Southern Chile. *Aquatic Mammals* 31 (2): 234-242
- Richards, D.G. (1981) Alerting and message components in songs of rufous-sided towhees. *Behaviour* 76: 223-249
- Richardson, W.J, Greene Jr., C.R., Malme, C.I., Thomson, D.H. (1995) *Marine mammals and noise*. Academic Press, San Diego, C.A.
- Richter, C., Dawson, S., Slooten, E. (2006) Impacts of commercial whale watching on male sperm whales at Kaikoura, New Zealand. *Marine Mammal Science* 22 (1): 46-63
- Romanenko, E.V. (2004) Some Results of Studying the Acoustics of Dolphins. *Acoustical Physics* 50 (3): 343-349
- Rossi-Santos, M.R., Podos, J. (2006) Latitudinal variation in whistle structure of the estuarine dolphin *Sotalia guianensis*. *Behaviour* 143: 347-364
- Scarpaci, C., Bigger, S.W., Corkeron, P.J., Nugegoda, D. (2000) Bottlenose dolphins (*Tursiops truncatus*) increase whistling in the presence of "swim-with-dolphin" tour operations. *Journal of Cetacean Research and Management* 2 (3): 183-185
- Scott, M.D., Chivers, S.J. (1990) Distribution and Herd Structure of Bottlenose Dolphins in the in the Eastern Tropical Pacific Ocean. In *The Bottlenose Dolphin*. eds. Leatherwood, S., Reeves, R.R. Academic Press, Inc. San Diego, California. pp. 387-402
- Shane, S.H. (1990) Behavior and Ecology of the Bottlenose Dolphin at Sanibel Island, Florida. In *The Bottlenose Dolphin*. eds. Leatherwood, S., Reeves, R.R. Academic Press, Inc. San Diego, California. pp. 245-265

- Smolker, R.A., Richards, A.F.; Pepper, J.W. (1992) Sex differences in patterns of association among ocean bottlenose dolphins. *Behaviour* 123: 38-69
- Tyack, P. (1986) Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behavioral Ecology and Sociobiology* 18: 251-257
- Untersteiner, H. (2005) *Biostatistik: Datenauswertung mit Excel und SPSS für Naturwissenschaftler und Mediziner*. Facultas Universitätsverlag, Wien, Austria
- Van Opzeeland, I.C., Corkeron, P.J., Leyseen, T., Similä, T., Van Parijs, S.M. (2005) Acoustic behaviour of Norwegian Killer Whales, *Orcinus orca*, During Carousel and Seiner Foraging on Spring-Spawning Herring. *Aquatic Mammals* 31 (3): 110-119
- Van Parijs, S.M. and Corkeron, P.J. (2001) Boat traffic affects the acoustic behaviour of Pacific humpback dolphins, *Sousa chinensis*. *Journal of the Marine Biological Association of the United Kingdom*. 81: 533-538
- Verfuss, U.K. (1996) Jagd- und Echoortungsverhalten eines Amazonasflußdelphins (*Inia geoffrensis*) in Gefangenschaft. Diplom thesis University of Tübingen, Germany
- Weihs, D., Webb, P.W. (1984) Optimal Avoidance and Evasion Tactics in Predator-Prey Interactions. *Journal of Theoretical Biology* 106: 189-206
- Wells, R.S., Boness, D.J., Rathbun, G.B. (1999) Behavior. In *Biology of Marine Mammals*. eds. Reynolds III, J.E., Rommel, S.A. Smithsonian Institution, Washington D.C. pp. 324-422
- Yan, Z., Niezrecki, C., Beusse, D.O. (2005) Background noise cancellation for improved acoustic detection of manatee vocalizations. *Journal of the Acoustic Society America* 117 (6): 3566-3573