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**Humpback whale habitat preference and occurrence of songs in
relation to depth and sea bottom structure off the coast of
Esmeraldas, Ecuador**

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RESUMEN

La costa del Pacífico de Perú, Ecuador, Colombia y Panamá son importantes áreas de reproducción para las ballenas jorobadas, donde se aparean, dan nacimiento y amamantan a sus crías. Parte de la costa de Esmeraldas, al norte del Ecuador fue establecido como una reserva marina en Octubre del 2008, con la finalidad de proteger una parte del área reproductiva de esta especie y biodiversidad marina presente en la misma. El área se encuentra localizada junto a uno de los mayores puertos marinos del Ecuador (Balao), donde el petróleo de la Amazonía es transportado hacia varios destinos alrededor del mundo. Las actividades producidas por el hombre están creciendo constantemente en los ambientes marinos, incluso la contaminación acústica causada por exploraciones de gas y petróleo y tráfico marino. Información sobre las características de hábitats claves para los cetáceos y su distribución son necesarias para atender medidas de conservación y explicar procesos ecológicos. La profundidad y composición de fondo marino son considerados parámetros ambientales estáticos que podrían ser utilizados para entender la preferencia de hábitat y comportamiento acústico de estos animales. En este estudio, nosotros investigamos la relación y distribución de grupos sociales de ballenas jorobadas y ocurrencia de cantos dentro del área de estudio, basado en profundidades (hasta 200 m), y tipo de fondo marino (blando y mixto). Los grupos de parejas, solitarios, y grupos con una cría, no mostraron fuerte tendencia a un cierto tipo de sustrato o profundidad. Sin embargo, los análisis espaciales revelaron que todos los grupos mostraron una leve o moderada agrupación en su distribución. Grupos con una cría mostraron una preferencia hacia un sustrato mixto, mientras los grupos competitivos en general presentaron una baja preferencia por algún tipo de profundidad o sustrato. Considerando que se pudieron grabar canciones de las ballenas jorobadas con frecuencia por todo el área de estudio. Los análisis mostraron que individuos cantantes estuvieron distribuidos al azar y no se agrupan en el área de estudio. Esto sugiere que ballenas cantantes no parecen seleccionar algún tipo de sustrato marino o profundidad para emitir sus cantos. Sin embargo, los cantos fueron registrados con mayor frecuencia en aguas poco profundas cercanas a la costa, en comparación con aguas profundas del área reproductiva. Por lo tanto, la costa de Esmeraldas podría representar un hábitat clave y vital para la población de ballenas jorobadas en el Pacífico sudeste.

ABSTRACT

The Pacific coast of Peru, Ecuador, Colombia and Panama are important humpback whale wintering grounds where they mate, give birth and nurse their young. Part of the coast off Esmeraldas, in the North of Ecuador, was established as a marine reserve in October 2008 in order to protect part of this breeding area and the marine biodiversity within it. This breeding area is located next to one of the most important ports in Ecuador (Balao), where oil from the Amazon is shipped to various destinations around the world. Human activity is constantly growing in the marine environment including sound contamination caused by oil and gas exploration and maritime traffic. Information on the characteristics of key habitats for cetaceans and their distributions are needed to assist in conservation measures and explain ecological processes, where depth and bottom composition are considered static environmental parameters that could be used to understand habitat preference and behavior acoustic. In this study, we investigated the relationship and distribution of humpback whale social groups and the occurrence of song within the study area in relation to depth (up to 200 m), and substrate type (muddy soft and mixed). Groups of pairs, singletons, and groups with a calf not showed a strong sloped over type bottom and depth. However, spatial analyses revealed all social groups showed a low or moderately clustered distribution. Groups with a calf showed particular preference to mixed bottom substrates, whereas competitive groups displayed a low overall preference for bottom type or depth. Whereas, humpback whale songs were could be recorded frequently for all the study area. Our analyses showed that singers were randomly distributed and were not clustered over the study area. This suggests that singers do not appear to be selecting bottom type or depth. However, songs were recorded more often in shallow water than offshore in this wintering ground. The coast of Esmeraldas could therefore represent a core and vital habitat for the Southeastern Pacific population of humpback whales.

TABLE OF CONTENTS

| | |
|--|----|
| RESUMEN | 5 |
| ABSTRACT | 6 |
| INTRODUCTION | 11 |
| MATERIAL AND METHODS | 16 |
| <i>Study Area</i> | 16 |
| <i>Data Collection</i> | 16 |
| <i>Identifying Social Groups</i> | 17 |
| <i>Acoustic Recordings</i> | 17 |
| SPATIAL AND STATISTICAL ANALYSES | 18 |
| <i>Preparation of the Data</i> | 18 |
| <i>Social Groups</i> | 19 |
| <i>Song Levels</i> | 21 |
| RESULTS | 24 |
| <i>Social Groups</i> | 24 |
| <i>Sightings of Social Groups with Depth and Substrate</i> | 24 |
| <i>Distribution of Social Groups</i> | 25 |
| <i>Song Occurrence spatial analyses</i> | 25 |
| DISCUSSION | 27 |
| <i>Social Groups Sightings</i> | 27 |
| <i>Social Groups vs. Depth and Substrate</i> | 29 |
| <i>Song with Depth and Substrate</i> | 31 |
| CONCLUSIONS | 35 |
| REFERENCES | 37 |
| APPENDIX I Tables: | 46 |
| APPENDIX II Figures: | 49 |

TABLES AND FIGURES

Tables Appendix I

Table 1. Definitions of humpback whales social groups encountered on the Esmeraldas Coast in 2012.

Table 2. Occurrence of humpback whale songs according to depth. SNR (*signal to noise ratio*): vg= very good; g= good; a= average; p= poor; vp= very poor; ns= no song.

Table 3. Average Nearest Neighbor analysis (NNA) of humpback whale social groups. Index values above 1 represent a random distribution, and values less than 1 represent a clustered distribution.

Table 4. Moran's Index and Getis-Ord General G-Index analysis of humpback whale song.

Figures Appendix II

Figure 1. Map of the eastern South Pacific region. The study area was located on the Coast of Esmeraldas (Bajos de Atacames), Ecuador.

Figure 2. Humpback whales survey effort from 2012 (June to August) over bathymetry off the coast of Esmeraldas.

Figure 3. Humpback whale social group distribution according to geographic bathymetry and bottom composition.

Figure 4. Frequency spectrogram from recordings of very good and very poor song quality.

Figure 5. Social groups of humpback whales and percentage in Bajos de Atacames.

Figure 6. Percentage of sightings of every humpback whale social group among depths. (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

Figure 7. Percentage of sightings of every humpback whale social group between bottom type. (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

Figure 8. Percentage of sightings for all humpback whale social groups by depth. (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

Figure 9. Percentage of sightings for all humpback whale social groups by substrate type (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

Figure 10. Ripley's K-Function of the overall humpback whale distribution off Esmeraldas during 2012. The observed K-function is higher than the expected indicating a clustered distribution.

Figure 11. Occurrence of humpback whale song based on depth (0 to > 100 m) and bottom composition (mixed/muddy soft). Level of song very good (2 km) and good (5 km) are presented with buffers where potentially singers were singing.

Figure 12. Behavior and social groups during acoustic surveys: traveling, pectorial slapping, tail slapping, breaching, mother-calf and pairs.

INTRODUCTION

The large baleen whales or Mysticetes are broadly distributed throughout the world's ocean basins. Mysticete whales appear along the continental shelves and in pelagic offshore waters, but also conduct extended transoceanic migrations during their life cycle. For example, humpback whales (*Megaptera novaeangliae*) migrate from feeding grounds located in polar oceans to their wintering grounds in tropical and subtropical waters (Clapham, 2000). Humpback whales are characterized by sexual dimorphism; females are larger than males and both reach sexual maturity between five and seven years of age (Clapham, 1996). Females have a gestation period of 11 to 12 months and an inter-birth interval of approximately two years (Clapham, 2000). Overall, humpbacks are easily identified through long flippers, acrobatic behavior, and remarkable tail patterns (Katona & Whitehead, 1981; Clapham, 2000).

Wintering ground destinations commonly are located in many coastal regions around of world. One important region is located in the Southeastern Pacific, which has been relevant some of the humpback whales that arrived from Antarctic Peninsula and a part of South America (Magallanes Channel) (Gibbons et al., 2003; Stevick et al., 2004). Humpback whales from these feeding areas form a group called Stock G under the International Whaling Commission (IWC, 2006), which migrate to wintering grounds located in Peru, Ecuador, Colombia and Panama (Southeastern Pacific) (Flórez et al., 2007). In this sense, the movement of humpback whales and site fidelity through re-sightings have allowed scientist to identify relevant wintering grounds with individual whales of different populations that arrive from summer feeding areas in Antarctica (Stevick et al., 2004).

Currently, the red list of endangered species of the International Union for Conservation of Nature (IUCN) classified the humpback whale as “Least Concern” (Reilly, 2008). However, now it is necessary to improve information regarding estimations of sub-populations around our oceans. For example, the current population estimate for humpback whales in western South America is 2,900 (95% CI= 2000 – 4200) although this estimate was calculated using only two years of data (see IWC, 2013 <http://iwc.int/estimate>). This stock has suffered from a long period of historical whaling from the coast of the Southeastern Pacific to Antarctica (Area I Eastern) and commercial whaling affected the majority of this stock during the 20th century (Chapman, 1974).

Some Mysticetes such as Right, Gray and Humpback whales are known for their specific breeding grounds, supported by their migratory behavior (Bannister, 2002). Wintering grounds for humpback whales in tropical areas are identified commonly in near-shore regions (Clapham, 2000), although home range knowledge is minimal due to limited observer effort in several areas farther offshore. On the other hand, other cetaceans such as blue whales could present alternative life strategies to feeding and reproduction processes in tropical and subtropical areas that could possibly occur together, when whales migrate from high-latitudes (Hucke-Gaete, 2004). However, specific wintering destinations for example of Blue, Minke, Sei and Fin whales are still poorly understood (Reilly & Thager, 1990 Kasamatsu et al., 1955; Best 2003; Tetley, 2004).

The presence and distribution of humpback whales around the world today is influenced by social issues (Ersts & Rosenbaum, 2003), biological requirements (Craig & Herman, 2000), and environmental parameters (Hooker et al., 1999; Rasmussen et al., 2007). Local geographical, environmental and oceanographic parameters can help to explain habitat preferences and possibly other ecological parameters. In particular, depth appears to be relevant to the distribution of some species of cetaceans (Hooker et al., 1999; Cañadas et al., 2002; Azzelino et al., 2008). For humpback whales on their subtropical/tropical wintering grounds, there is little knowledge of the explanation that could support such distribution patterns (Craig and Herman, 2000). Studies indicate, including those conducted in Ecuador, that mother and calf pairs commonly prefer shallow water up to 20 m (Martins et al., 2001; Félix & Haase 2001a, b, 2005; Ersts & Rosenbaum, 2003; Félix & Botero, 2009), whereas singletons, pairs, competitive groups and singers have been observed from 10 to 60 m in depth (Martins et al., 2001; Félix & Haase, 2001a, b; Oviedo & Solís, 2008). However, in the wintering grounds located off the central American Pacific coast and the Hawaiian Islands, groups with calves and singers can be commonly observed in offshore waters (e.g. up to 200 m) (see Frankel et al., 1995; Rasmussen et al., 2011; Cartwright et al., 2012).

When examining the acoustic behavior of cetaceans such as humpback whales in relation to environmental parameters, many factors affect sound propagation and broadcasting of the signal (Richardson et al., 1995). In other words, it is possible that oceanographic features and topography may influence the pattern of vocal occurrence from humpback whales in the breeding grounds (Tyack, 2000). Sound transmission and propagation can be affected by changes in temperature, salinity, and pressure which vary with depth and bottom composition (Jensen & Kuperman, 1983; Richardson et al., 1995).

Simulations of song propagation have shown that individual position, output of frequency, depth and bottom composition can all influence the propagation and broadcast of the optimum frequencies of humpback whale song (Mercado & Frazer, 1999). Studies have shown that sound over soft bottom sediments is absorbed rapidly, whereas over sandy bottoms sound is more refractive (Jensen & Kuperman, 1983; Mercado and Frazer, 1999). For example, most occurrences of singing have been recorded between 15 to 60 m deep (see Whitehead & Moore; 1982; Rasmussen et al., 2011). However, there are minimal differences in the distribution of singers and depth range on the northwestern coast of Hawai'i (see Frankel et al., 1995), and a slight preference of singers for flat seafloors with a sandy bottom (Cartwright et al., 2012). At certain archipelago areas (bays), songs have been frequently recorded over shallow water and smooth bottoms (see Whitehead & Moore, 1982). However, depth appears to overlay other factors, such as bottom composition and there is little knowledge about the constraints of humpback whales songs and environmental parameters (Mercado & Frazer, 1999).

Male humpback whales produce a complex, stereotyped, repetitive breeding display termed 'song' (Payne & McVay, 1971). Although the exact function of song is still debated, song is produced typically by single males (Glockner, 1983; Frankel et al., 1995; Tyack, 2000), and may act as a sexual advertisement to females or territorial spacing between males in the breeding grounds (Winn & Winn, 1978; Tyack, 1981; Tyack & Whitehead, 1983; Frankel et al., 1995; Helweg et al., 1992; Clapham, 1996; Darling & Berube, 2001; Smith et al., 2008). Other hypotheses for song function include that song could be used as sonar to find females, obtain information about the marine environment and recognize other individuals (Tyack, 1997; Frazer & Mercado, 2000; Mercado & Frazer, 2001).

Anthropogenic sounds produced from human activities are potential threats to humpback whales when they migrate along continental shelves (Flórez et al., 2007). Acoustic pollution from exposure to sonar, tourism, commercial maritime traffic and oil exploration have been rapidly growing in the oceans (Richardson et al., 1995), and has increased by 15 decibels over the last 50 years (Firestone & Jarvis, 2007). So far no major attempts have been made to reduce the threats of sound pollution for the highly acoustic marine mammals within the region, but underwater noise can have dramatic effects on marine mammal populations (see Fernández et al., 2005; Weilgart, 2007; Parsons et al., 2008; Kvadsheim et al., 2012). Even though the CPPS (Comisión Permanente del Pacífico Sur) adopted a marine mammal action plan, neither habitat selection nor sound contamination has been taken into account (Flórez et al., 2007). Therefore, information on natural habitat preference, social groups, and acoustic behavior in relation to environmental characteristics and underwater sound is crucial to understanding the biological fitness of this population (Gaillard et al., 2010; Beyer et al., 2010), and develop efficient elements for conservation management of humpback whales.

The habitat preference of different social groups and the occurrence of songs in the humpback whale breeding ground off the coast of Esmeraldas were studied with the following objectives:

- 1) determine the spatial distribution of humpback whale social groups in relation to depth and bottom composition; 2) identify the social group stratification of humpback whales in this wintering ground; and 3) describe the spatial distribution of singers in relation to depth and bottom composition in the study area.

MATERIAL AND METHODS

Study Area

Northern Ecuador is one of the multiple breeding locations for the humpback whales that migrate up the west coast of South America (Group G) (IWC, 2006). Our field site covered the Esmeraldas coast from the Esmeraldas River (N 0°59'54,1'';W 79°38'37,7'') to Punta Galera (N 0°49'10.15" , W 80°02'55.67") (Fig 1). We surveyed from the coast to the 200 m depth contour which extends over 196.019, 39 ha on the continental platform with approximately 70 km of coastline. Bajos de Atacames as is called this study area presents a broad sub-range of climates, due to the influence of the Panamic oceanic current and Equatorial Undercurrent (INOCAR, 2005). Sea surface temperatures range between 24 to 26 ° C throughout the year. The seabed structure is composed of areas with hard substrates, mixed bottoms formed of sand and rock, walls with rocks and soft bottoms with muddy channels, with depths ranging from 10 to 60 m (Denkinger et al., 2006).

Data collection

Humpback whale surveys were conducted for 32 days, between June and August 2012, using an 8 m fiberglass vessel powered with a 75 HP outboard engine as the observation platform. Eye height was approximately at 2.50 m above sea level and the survey speed ranged from 25 to 30 km/h. Daily 5 to 6 hour transects (N = 12 transects) were conducted randomly covering the entire research area with a standardized ad hoc acoustic sampling effort every 25 to 30 minutes (N = 20 recordings) (Fig 2), and occasionally whenever humpback whales were sighted.

At each sighting the group or individual was approached for data collection (genetic, photo-identification and acoustic sampling). At each sighting, the start and end time of the observation, geographic position, group size, presence of calves and behavior was recorded. The songs were recorded for 30 minutes or more, when good singers were present, or from 5 to 15 minutes when songs were present to confirm quality recordings or absence of songs.

Identifying social groups

Social groups were identified through typical and obvious behaviors, such as timing of blows, surfacing, and aerial acrobatics characteristic of this species (Whitehead, 1983). Movements, such as synchronized diving, swimming speed and heading improved the identification of social groups (Clapham, 1993b). A detailed description of group identification is given in Table 1.

The sex of animals was not determined in this study except behaviorally. Singers were presumed to be male and the closest animal to a calf was presumed to be its mother, thus female. Moreover, within competitive groups, the nuclear animal was presumed to be a female and the principal and secondary escorts as males (see Glockner-Ferrari & Ferrari, 1985; Clapham et al., 1992).

Acoustic recordings

For each recording, the position was identified using a handheld GPS unit (Garmin Legend). A H2a-XLR omnidirectional hydrophone (whose receipt is basically independent of the incident sound wave's angle of arrival), with a reception sensitivity of -180 dBV/uPa +4 dB from 20 Hz to 100 kHz (<http://www.aquarianaudio.com/hydrophones.html>), with string wrapped in a long spiral around the cable to reduce vibration noise was submerged to 7-8 m depth (E. C. Garland personal communication), while the boat was stopped and the motor

was turned off. This process was carried out every 25 to 30 minutes using line transects, and the remaining recordings were taken ad hoc throughout the area (Fig 2) (Rasmussen et al., 2011). Acoustic samples were recorded on a Tascam DR-40 tape recorder, set for recording WAV files at 44.1 kHz and 16 bit. Songs were recognized from the distinctive species-typical harmonic sounds, long vocalization times and repeating patterns (Payne & McVay, 1971). Volume, sea state, presence of whales, behavior, submarine sounds, and start and end time of recordings were noted.

SPATIAL AND STATISTICAL ANALYSES

Preparation of the Data

Multiple distances were scanned from the boat to identify social groups within the area (e.g. distance intervals of 100 m, 300 m, 500 m, 800 m, 1 km, and up to 5 km). Data from mother-calf and mother-calf-escort groups were combined into a single category, called groups with a calf, due to data constraints (small simple size). Only groups sighted within 100 m of the boat (N = 154) and all song recordings (which were considered independent events) were included in spatial analysis in order to decrease any spatial autocorrelation between multiple records (MacLeod et al., 2007). Geographic positions of both sightings (social groups), and acoustic recordings were mapped on a chart including seafloor composition, and depth to obtain these (estimated) parameters after each sighting or recording (see Denkinger et al., 2006).

Acoustics samples were categorized into five quality levels, according to humpback whales signal to noise ratio (SNR), or sound clearness versus background noise (E. C. Garland personal communication) (Table 2). Moreover, to assign recordings to one of the five levels from very good to very poor, we used Audacity 1.3 Beta and categorized the recordings according to sound pressure levels (dB) and frequencies (Hertz) (Fig 4). Finally, a Geographical Information System (GIS) was used to carry out exploratory spatial analyses, based in geographical environmental parameters (i.e. depth and bottom composition) (Manly et al., 2002).

Social groups

To determine social group stratification and autocorrelation based on depth and bottom composition, humpback whale distributions were analyzed using ESRI ArcGis10. Our null hypothesis (Ho) was that there is not a clustered distribution of all social groups.

Here, Point Pattern Analysis (Ripley's K Function) was carried out using distribution values to establish if social groups were clustered or dispersed within the study area. This method creates a circle using a radius of a given length from every point (observation point), and counts the number of observations within this radius to obtain an average number of observations per circle (see Johnston et al., 2001; Lloyd, 2007). Social group stratification was calculated through the comparison of empiric observations and random distributions, with the following equation:

(1)

$$K(t_s) = \frac{A}{N^2} \sum_{i=1}^N \sum_{j \neq i} I(t_{ij})$$

Where,

$K(t_s) =$ average of points to a radius of a circle centered on a point in the pattern

(band interval distance)

$N =$ total number of points in study area

$A =$ plot area

$W_{ij} =$ weighting factor to correct for edge effects

$I(t_{ij}) =$ point numbers j around of point i with radius t and selected radius s .

The cumulative spatial distribution within social groups throughout the study period in relation to depth and bottom structure was evaluated using a Nearest Neighbor Analysis (NNA). The fundamental basis to NNA measures the distance among each data points centroid, and its' nearest neighbor's centroid location. This index is expressed as a ratio of the observed distance divided by the expected distance (based on a random distribution with the same number of data points) (Johnston et al., 2001). This analysis was carried out to evaluate if there was a clustered or random distribution pattern within social groups. NNA is considered an exploratory spatial analysis as changes in the survey area affect the model. However, NNA assumes that all measured points are independent and can be located anywhere within the study area (Johnston et al., 2001). The evaluation of autocorrelation to every social group could indicate a possible preference or lack thereof based on depth and bottom composition in the study area. The Nearest Neighbor index (R) was calculated using the following equation (McGrew & Monroe, 2000):

(2)

$$R = \frac{\overline{\text{NND}}}{\text{NNDR}} \quad \text{and} \quad \overline{\text{NNDR}} = \frac{1}{2 \sqrt{\frac{(n)}{A}}}$$

Where,

| | |
|----------------------------|--|
| $\overline{\text{NND}}$ = | sum of all nearest neighbor distance by n |
| $\overline{\text{NNDR}}$ = | average nearest neighbor distance for a random arrangement |
| n = | total number of point events |
| A = | total area |

Song levels

Here, we assumed that singers could be located potentially up to 5 km away but were more likely to be within 1 to 2 km of the recording location (E. C. Garland personal). Our analyses of humpback whale songs were based on very good (vg) and good (g) quality recordings only.

In the wintering grounds males are typically found singing while stationary, but are capable of singing while moving (as demonstrated on migration) (e.g. Noad & Cato, 2007). Moreover, song may act as a sexual advertisement to females, and/or male social sorting and potentially spacing on the breeding grounds (e.g. Helweg et al., 1992; Frankel et al., 1995; Darling & Berube, 2001; Darling et al., 2006). Song recordings (very good and good quality only) were considered independent events. Here our null hypothesis (Ho) was that there is not a clustered distribution of song recordings (singers) in this study area.

To analyze the overall spatial distribution of singers, Moran's Index and the Getis-Ord General G-Index were used to examine autocorrelation. Moran's Index allows for evaluation of the extent of autocorrelation within local neighborhoods of sampling data (Lloyd, 2007), while the Getis-Ord General G-Index can identify local concentrations of animals, and define whether values are displaying strong clustering above or below the average (Getis & Ord,

1992, 1996). Evaluation of song autocorrelation could indicate a preference to particular depths and/or bottom compositions within the study area. To calculate Moran's Index, a spatial similitude value is first established using the equation:

Similitude value

$$S_{ij} = (x_i - \bar{x})(x_j - \bar{x}) \quad (3)$$

From this, Moran's Index is calculated using the equation:

Index I

$$I = \frac{\sum_{i=1}^n \sum_{j=1}^n \omega_{ij} (x_i - \bar{x})(x_j - \bar{x})}{\sigma^2 \sum_{i=1}^n \sum_{j=1}^n \omega_{ij}} \quad (4)$$

Where,

| | |
|-----------------|--|
| $n=$ | number of features measured |
| $x_i=$ | value of feature i , |
| $x_j=$ | value of feature j , |
| $\bar{x} =$ | mean value of all features |
| $\omega_{ij} =$ | weight assigned to each pair of features |

Weighting Parameter

$$\omega_{ij} = \frac{1}{d_{ij}} \quad (5)$$

The Getis-Ord General G-Index is calculated following Mueller-Warrant et al. (2008):

(6)

$$G = \frac{\sum_i \sum_j w_{ij} (x_i * x_j)}{\sum_i \sum_j (x_i * x_j)}$$

Where,

x_i = value of feature i ,

x_j = value of feature j , and

w_{ij} = spatial weight assigned to each pair of features x_i, x_j

Whereas, the Getis-Ord General G for values distributed randomly was calculated with the following equation:

(7)

$$\frac{\sum_i \sum_j w_{ij}}{n(n-1)}$$

Where,

w_{ij} = spatial weight between

i, j = features

n = total number of points events

RESULTS

Social groups

A total of 579 whales were observed in 304 sightings with a group size ranging between one and eight individuals, with an average of 1.90 individuals per sighting (SD = 1.12, N = 304). Of the 304 observations, only sightings observed within a range of 100 m (N = 154) were included in the spatial analyses. Most of the whales observed were singletons (42 %) and pairs (33 %), while mother-calf pairs comprised 5 %, mother-calve-escorts 8 %, and competitive groups 13 % (Fig 5). The majority of groups observed were surface active groups (N = 98), while fewer groups were sighted while moving (singletons N = 19, pairs N = 21, competitive groups N = 8, mother with a calf N = 8) and all groups showed a trend towards the northeast coast (Fig 3).

Sightings with depth and substrate

More than half of the sightings were recorded in shallow water less than 20 m deep (62 %; 95 of 154) and on mixed substrate (65 %; 89 of 137) (Fig 3). For all social groups (singletons, pairs, groups with a calf and competitive groups), each was sighted over 50 % of the time in depths of less than 20 meters (Fig 6) and the majority of sightings for each social group were over a mixed bottom (Fig 7).

For each depth bin, pairs, singletons, and groups with a calf were sighted the majority of the time at < 20 m (Fig 8). Pairs and singletons were more frequent at 20-50 m, while pairs and competitive groups were more frequent at >50 m compared with singletons and groups with a calf (Fig 8). Pairs and singletons were sighted more often over mixed substrates than all other groups (Fig 9); over the muddy soft substrate, singletons and pairs showed similar values, but these were more frequent than groups with a calf and competitive groups (Fig 9).

Distribution of groups

Throughout the study period the overall humpback whale group distribution was clustered over certain depth and bottom structure ranges within the study area (NNA index value = 0.72, Z-Score = -6.55, $p < 0.01$, and Ripley's K-Function) (Fig 10). However, among social groups, competitive groups were more dispersed, whereas singletons and groups with a calf were considered to exhibit low clustering, and pairs were moderately clustered (Table 3). The clustered distribution within groups was not statistically significant ($p > 0.05$), except for groups of pairs ($p < 0.01$, index value = 1.026) (Table 3).

Results from spatial analysis showed a low and moderately clustered distribution and a slight segregation of group types (i.e. groups with a calf, and singletons) was observed across the study area (Fig 3). Singletons showed a preference for 10 to 20 m depth, while groups with a calf preferred shallower water with depths of 0 to 20 m, and pairs showed moderate clustering with a preference for 20 to 30 m depth (Fig 3). Moreover, groups of pairs, singletons, and groups with a calf showed particular preference to mixed bottom substrates (Fig 3), whereas competitive groups showed a dispersed pattern, indicating low or no preference for a particular bottom type or depth (Fig 3).

Song occurrence spatial analyses

From a total of 143 recordings of humpback whale songs, 23% were of a very good and good quality, and included in further analyses (Table 2). The distribution of songs was mapped according to depth and bottom composition (Fig 11). Songs were more frequently recorded on a mixed bottom substrate and in depths of less than 20 m (Table 2). This may be the result of uneven effort as most recording was focused in shallower water with only occasional trips

offshore to > 50 m. However, spatial analyses suggested that these songs from humpback whales were more randomly distributed than clustered (Table 4, Fig 11). In this study, songs of a very good quality were assumed to be from singers potentially up to 2 km or less from the boat, and songs of a good quality up to a maximum of 5 km away (E. C. Garland personal communication) (Fig 12).

Singers do not appear to be selecting bottom type or depth consistently (Fig 11). On average from our high quality recordings, there were two individuals visible during recording (SD = 1.16, n = 33) and the mean distance of whales observed from the boat was 300 m (SD = 608.75, n = 33).

Fifty-two percent of the recordings contained multiple singers, and 48 % single singers. While recording located singers, we observed surface activities, singers passed below the boat, were traveling while singing and singers were part of mother-calf-escort groups. Other behaviors such as tail slapping, pectoral slapping, breaching and lobtailing were often observed during the acoustic surveys and may or may not have been made from the group containing the singer(s) (Fig 12).

DISCUSSION

Migration patterns of humpback whales from coastal areas, islands and reef systems are studied broadly around ocean basins. Most of the studies concentrated in density estimate of this specie during winter season in tropic and sub-tropic environments (Clapham, 2000). While social and acoustic behaviour was analyzed in relation to geographical environmental parameters such as bottom composition and depth, which is necessary to understand and improve information about distribution patterns of cetaceans (Evans, 2008).

The distribution of humpback whales (social groups) can be used to determine possible habitat preference inside a wintering ground. Our results based on spatial analysis allowed to evaluate concentrations or dispersion of various social groups identified. We suggest inside the study area a slight preference and segregation of groups when whales arrive at this part of Southern Pacific.

Social group sightings

Classification of social groups based on surface activity (e.g. lobtailing, breaching, tail slapping, flippering and jumping constantly), together with on synchronized diving, swimming speed and temporal stability of humpback whales allowed identification of groups. The pairs and singletons social groups were more frequently observed within the study area than groups with a calf or competitive groups. These results have been observed at some Hawaiian wintering grounds. For example, pair groups have shown to maintain an association more stable than other social groups (Mobley & Herman, 1985) and suggest that this association is formed by sexually mature males and females with the intention of mating (Tyack & Whitehead, 1983; Mobley & Herman, 1985; Valsecchi et al., 2002). Hence, the

social group of pairs in our study area, possibly could have increased the probability of be registered more of one time.

The singletons social group was commonly observed, displayed broad movements (e.g. acrobatic breaching, tail slapping, jumping), which are associated to attract mates possibly (Mobley & Herman, 1985). This social group is associated by males individuals, which are commonly observed on the breeding grounds and individual females (e.g. Craig & Herman, 1997). Males may migrate to different breeding grounds and females possibly don't complete their migrations to tropical areas (Dawbin, 1966; Palumbi & Baker, 1994; Brown et al., 1995; Graig & Herman, 1997). Inside of this breeding ground high site fidelity of solitary males could occur, but more efforts are necessary to determine this issue (Ciolfi, 2013).

Competitive groups showed a low frequency, although there was a similar occurrence with groups with a calf. Affiliates of competitive groups with/without a calf, suggest that these are briefly composed of females, calf, males escorts or non-pregnant females during a wintering midseason (Mobley & Herman, 1985). Our surveys were carried out until midseason according to the migration of whales in the Southern Hemisphere (August). Taking into account that to end August and September mothers and calves can be commonly found in this breeding ground with/without escorts (J. Denkinger personal communication). This could explain the lower frequencies of mother, calf and escort groups registered in our surveys.

The social structure of humpback whales on wintering grounds in the Southern Hemisphere is reported sparingly. However, studies are generally consistent with our outcomes, for example, in Brazil, pairs and singletons were more frequently observed during the season, while competitive group and groups with calves displayed low densities (Martins et al.,

2001). Moreover in Antogil Bay, Madagascar, higher frequencies (66%) of pairs and groups of three or more whales have been reported as with mother-calf-escort groups (12%) (Ersts & Rosenbaum, 2003). While on the Southeast Pacific coast from Panama to Guatemala, the density and concentration of social groups on the breeding grounds is thought to be influenced by the migrations patterns of the populations while in feeding areas (see Rasmussen et al., 2011).

Social groups vs. depth and substrate

Distribution of social groups was associated with environmental parameters such as depth and bottom composition and spatial analysis was carried out to identify temporal patterns of distribution and preferences in this local wintering ground at off the coast of Esmeraldas.

The groups of mother-calf pairs and mother-calf-escort groups unified in groups with a calf showed strong preference for shallow water less than 20 m and 10 m, which may provide additional shelter and protection from prospecting males and predators (Corkeron & Connor, 1999). Here possible biases were presented to this distribution as it combined two different behavioral conditions, one which represents a prime mating opportunity and the other calving and nursery habitat (Smith et al., 2012). Our results showed that groups with a calf displayed a clustered distribution as they were more frequently found in shallow water in this study less than 20 m (79%) and over mixed substrates (70%). The distribution of humpback whales on other wintering grounds indicated that social group stratification and clustering occurs based on environmental parameters. Females with calves, singletons and singers at Osa Peninsula, Costa Rica, displayed a clustered distribution and showed overlap in distribution range among these groups (Oviedo & Solis, 2008).

At Au'au Channel Hawaii groups of adults appear to avoid water depths of less than 40 m, while preference of mother with a calf has been reported in depths between 60 and 80 m and over flat and sandy substrates (Cartwright et al., 2012). Also, females with calves have been observed in calmer water and around coral heads at Silber Bank, West Indies 'Caribbean' (Whitehead & Moore, 1982). Possibly, other factors such as human activities are affecting the marine environment and the distribution of humpback whales. However, shallow water (less than 20 m) appears to be an important factor to mothers and calves on mainland coasts such as Ecuador and Costa Rica (Félix & Haase, 2001a, b, 2005; Oviedo & Solís, 2008), and around oceanic islands such as the Big Island, Hawaii (Smulter, 1994).

Results from the spatial analysis indicated there was partial support for the segregation of social groups, specifically singletons, pairs and groups with a calf (Fig 3). Singletons showed a preference for 10 to 20 m depth, while groups with a calf preferred shallower water with depths of 0 to 20 m, and pairs showed moderate clustering with a preference for 20 to 30 m deep (Fig 3). These groups of pairs, singletons, and groups with a calf, also showed a slight preference for a mixed bottom substrate (Fig 3). Whereas competitive groups displayed a more dispersed pattern, indicating there is no possible preference for either substrate type or depth (Fig 3). This lack of preference for depth or substrate type may be due to behavioral state or reproductive status (Craig & Herman, 2000). Males within competitive groups are attempting to gain mating access to a female (Mobley & Herman, 1985) and are not likely to be focusing on their location. The females are likely to be actively attempting to dislodge escorts and may be moving erratically with a disregard for location. However, competitive groups were commonly observed over deeper water, in our study (> 20 m), where it may be easier for the female to maneuver and males to engage in agonistic interactions (greater movements) than in shallow water (Erst & Rosenbaum, 2003), which can be constrained by

seabed structures such as coral heads (Whitehead & Moore, 1982) and large rocks (J. Denkinger personal communication).

Song with depth and substrate

A high occurrence of song was detected (5 out of 143 recordings did not detect song), strongly indicating this area represents a breeding ground. Typically there are only minor efforts undertaken to recognize zones of core acoustic habitat in marine species in regards to the possible impact from human activities (Clark et al., 2009, Hatch & Fristrup, 2009). Our results demonstrate songs were routinely recorded through sampling in both shallow (in our study < 20 m) and offshore waters (up to 200 m) off the coast of Esmeraldas. Autocorrelation analysis showed singers were more likely to be randomly distributed within the study area than clustered together. It is possible that singers may not indicate a preference for particular substrate types or depths in this region. However, singers were frequently recorded in depths less than 20 m and over mixed bottoms. This may be the result of uneven sampling effort as most effort was focused in shallower water with only occasional trips offshore to depths of 50 m to 200 m. However, other wintering grounds have reported slightly different patterns of occurrence. Singers together with groups with a calf were more commonly identified than all other social group types in depths of 20 to 49 m (Oviedo & Solís, 2008; Rasmussen et al., 2011), and further offshore (50 to 100 m depth), singers were more frequently noted than all other social groups off the coasts of Central America (Rasmussen et al., 2011). Singers displayed a clustered distribution at Osa Peninsula, Costa Rica, although no significant differences in distribution based on depth ($p = 0.58$) or slope ($p = 0.45$) were reported (Oviedo & Solís, 2008). Dispersion of singers has been observed in both the offshore and shallow waters off the northwestern coast of the 'Big Island' of Hawaii (Frankel et al., 1995). We recorded two very good singers in the offshore waters over 50 m in depth in the

southwest region of our study site (Fig 12). Singers may have already arrived in the area or migrated to other close by wintering grounds (Swartz, 2002).

On the wintering grounds in general most occurrences of song have been recorded between 15 and 60 m deep (see Whitehead & Moore, 1982; Rasmussen et al., 2011). On the northwestern coast of Hawai'i, there are minimal differences in the distribution of singers and depth range (see Frankel et al., 1995), and a slight preference of singers for flat, sandy bottoms (Cartwright et al., 2012). In a study by Whitehead and Moore (1982), singers were reported to have a preference for smooth bottom substrates (smoothest) which we did not find in the current study. Oceanographic features and topography may influence the pattern of vocal occurrence from humpback whales on the breeding grounds (Tyack, 2000). Sound transmission and propagation can be affected by changes in temperature, salinity, and pressure which vary with depth and bottom composition (Jensen & Kuperman, 1983; Richardson et al., 1995). Studies have reported that sound transmitted over soft bottom sediments is absorbed rapidly, whereas over sandy bottoms, sound is more refractive (Jensen & Kuperman, 1983; Mercado & Frazer, 1999). In shallow water the depth, slope/gradient and substrate type (among others) all interact to determine propagation and transmission of various optimum frequencies (Mercado & Frazer, 1999; Kuperman & Lynch, 2004).

Using spatial analyses to determine the distribution of singers on this winter breeding ground, we can weakly tie these propagation assumptions particularly in regards to substrate type to explain the locations of singing individuals. An important consideration that has not been explored is the interaction of singers with surrounding social groups and how this may affect the location of singing individuals. Singers may simply be broadcasting their song in higher density, core areas to increase the probability of being heard by conspecifics. This

aggregation to higher density areas may explain their wider location (i.e. this breeding ground), and within this, they are located in the mid-depth range (10-20 m) and over the substrate (mixed) frequented by females.

Typically humpback whale songs have been recorded on winter breeding grounds (Payne & McVay, 1971; Payne & Payne, 1985, Cerchio et al., 2001; Darling & Berube, 2001; Garland et al., 2011, 2012, 2013), but also occasionally on the summer feeding grounds (Mattila et al., 1987; Clark & Clapham, 2004; Stimpert et al., 2012, and extensively on migration routes (Clapham & Mattila, 1990; Noad et al., 2000; Noad & Cato, 2007; Smith et al., 2008). Breeding grounds around of the world suffer different grades of acoustic pollution; exposure to sonar, tourism vessels, commercial shipping, and oil and gas exploration have been rapidly growing in the oceans (Richardson et al., 1995; Parsons & Dolman, 2004) and have already caused an increase of 15 decibels above historical noise levels over the last 50 years (Firestone & Jarvis, 2007). Changes in acoustic behavior from anthropogenic noise have been demonstrated in baleen whales (e.g. Parks et al., 2010; Rolland et al., 2012; Risch et al., 2012). In humpback whales, changes in the occurrence of songs and their duration has been reported (e.g. Norris, 1994; Risch et al., 2012), and noise general indicates a significant source of stress on the breeding grounds (see Clapham & Mattila, 1993; Bauer et al., 1993). Therefore, the increase of noise exposure by shipping traffic could have harmful effects over marine ecosystems in coast zones specifically (see Merchant et al., 2012). Understanding the distribution and bioacoustics of highly vocal species is an important method for improving management and conservation of marine species, particularly cetaceans (Evans, 2008; Southall & Novacek, 2009; Laiolo, 2010).

Significant development of oil and gas exploration may occur along the coasts of the eastern South Pacific (Flórez et al., 2007). This increased development will increase interactions with marine life and may cause deleterious effects to individuals and populations. For example, off the coast of Peru, approximately 438 dolphins died and exhibited signs of acoustic impacts possibly from seismic oil exploration. However, the final report indicated this was not a direct impact (see IMARPE, 2012). Deleterious effects of dramatic noise pollution and how these can affect marine mammals have been highlighted from naval exercises and other sources of pollution (see Simmonds et al., 2004; Fernández et al., 2005; Parson et al., 2008).

Increasing anthropogenic activity along the coast of developing countries, such as Ecuador, can increase the noise pollution and present a serious threat for marine mammals that are highly acoustic. The coast of Esmeraldas has one of the most important ports for the region (Balao), where oil from the Amazon is shipped to various destinations around the world. The reliance of the world on oil is continuing to increase which will likely result in an increased maritime vessel traffic, and consequently noise, off the Esmeraldas coast.

Due to this increased marine traffic from commercial shipping and an active marine tourism industry, it is now essential to understand the vocalizations of humpback whales that frequent this breeding ground. Information on the natural habitat preference, social groups, and acoustic behavior in relation to environmental characteristics of humpback whales from long-term surveys and acoustic monitoring will allow an understanding of the biological fitness of this population, and help develop efficient conservation management of humpback whales and other marine mammals in this marine sanctuary.

CONCLUSIONS

Visual and acoustic monitoring of humpback whales' distribution while temporally close to the Pacific coast, allows the evaluation of habitat preferences and the occurrence of song at this wintering ground based on geographical and environmental parameters (i.e. depth and bottom composition). Sightings carried out jointly with acoustic monitoring of humpback whales recorded a large number of humpback whales as part of temporary social groups. Singletons and pairs were the most common social group observed off the coast of Esmeraldas. Spatial analyses revealed that singletons, pairs, and groups with a calf had a slight habitat preference and social segregation within this reproductive area. These groups displayed a habitat preference for shallower water. In addition, mother-calf and mother-calf-escort groups were observed more often in very shallow water (less than 20 m) which we suggest aids in protection of their young from predators or aggressive behavior from competitive groups, while competitive groups showed a more dispersed distribution indicating very little or no preference for a particular bottom type or depth. Moreover, singletons, pairs and groups with a calf were typically recorded over a mixed bottom composed of sand and rock, with rock walls. We know little regarding the start of their migration from Antarctic waters until they arrive at this wintering ground located at Bajos de Atacames. Hence, it is important to continue studies of humpback whales distribution from this and additional wintering grounds on the Ecuadorian coast.

The occurrence of songs from acoustic recordings showed a similar trend as social groups. Very good and good songs were commonly recorded in shallow water less than 20 m deep, and over mixed bottoms. However, spatial analysis suggested that singers were distributed in a more random arrangement than clustered together. Environmental parameters were linked

to the distribution of humpback whales, which could be used to understand habitat preference and acoustic behavior on this wintering ground. However, the inclusion of additional geographic and environmental parameters and social is required to carry out a more robust spatial analysis.

Noise pollution is increasing worldwide; it is therefore important to recognize areas of sound production. An essential first step is to encourage further research on this topic and develop management and conservation strategies for cetaceans, such as humpback whales, and their habitats in coastal development areas. The northern coast of Esmeraldas has significant whale watching vessel tourism, and an important port is close by where oil from the Amazon is shipped to various destinations around the world. Combined, this has the potential to significantly impact the marine reserve and negatively impact the humpback whale population that is temporally resident. This region represents an important wintering ground for the humpback whales of the Southeast Pacific. Behavioral and acoustic data indicate this is an important breeding ground through the presence of song which is a broadcast breeding display, the formation of competitive groups actively engaged in antagonistic behaviors in pursuit of a female, and finally, the presence of young calves. This study provides vital baseline information on the distribution of humpback whale social groups and occurrence of songs on this important breeding and calving ground for the Southeastern Pacific population. Results from this study should be incorporated into the management and conservation measures undertaken within this marine reserve to ensure the continued protection of humpback whales within Ecuador's waters.

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APPENDIX I: TABLES

Table 1. Definitions of humpback whales social groups encountered on the Esmeraldas Coast in 2012.

| Group type | Description | References |
|-------------------------|---|--|
| Singletons | Solitary animals. | Tyack and Whitehead, 1983 |
| Pairs | Two individuals with similar movements such as synchronized diving, swimming speed and direction. | Clapham, 1993b |
| Mother and calf | Individual accompanied by a calf of less than 8 m length. | Whitehead 1983; Clapham and Mead, 1999; Scheidat et al., 2000 |
| Mother, calf and escort | Individual (usually a male) accompanying a mother and calf. | Baker and Herman, 1984 |
| Competitive groups | Two or more escorts engaging in clear agonistic behavior between whales including aggressive and exaggerate lunges, throat expansion, physical contact (e.g. body blocking), bubbles streams by thrashes of the tail and commonly caused minor injuries, in the presence of a female with/without calf. | Tyack, 1981; Tyack and Whitehead, 1983; Baker and Herman, 1984; Clapham et al., 1992; Darling et al., 2006 |

Table 2. Occurrence of humpback whale songs according to depth. SNR (*signal to noise ratio*): vg= very good; g= good; a= average; p= poor; vp= very poor; ns= no song.

| Depth (m) | Number of recordings | SNR | | | | | |
|--------------|----------------------|-----------|-----------|-----------|-----------|-----------|----------|
| | | vg | g | a | p | vp | ns |
| < 20 | 73 | 10 | 14 | 27 | 12 | 8 | 2 |
| 20 - 30 | 29 | 4 | 3 | 5 | 5 | 12 | 0 |
| 30 - 50 | 6 | 0 | 0 | 0 | 5 | 1 | 0 |
| > 50 | 35 | 2 | 0 | 8 | 5 | 17 | 3 |
| Total | 143 | 16 | 17 | 40 | 27 | 38 | 5 |

Table 3. Average Nearest Neighbor analysis (NNA) of humpback whale social groups. Index values above 1 represent a random distribution, and values less than 1 represent a clustered distribution.

| Social groups | n | Observed Mean Distance (km) | Expected Mean Distance (km) | Z-Score | P-Value | Index Value | Pattern |
|--------------------|----|--------------------------------|--------------------------------|---------|---------|----------------|--------------------|
| Singletons | 40 | 0.023 | 0.023 | -0.179 | 0.857 | 0.985 | Clustered low |
| Pairs | 51 | 0.014 | 0.018 | -3.395 | 0.000 | 0.768 | Clustered moderate |
| Groups with a calf | 27 | 0.020 | 0.021 | -0.534 | 0.593 | 0.947 | Clustered low |
| Competitive groups | 19 | 0.030 | 0.029 | 0.250 | 0.802 | 1.026 | Dispersed |

Table 4. Moran's Index and Getis-Ord General G-Index analysis of humpback whale song.

| | n | Moran's Index | Expected Index | z-score | p-value | Confidence Interval | Pattern | Spatial Autocorrelation |
|---------------------------|----|--------------------|--------------------|---------|---------|---------------------|---------|-------------------------|
| Moran's I | 33 | -0.0231 | -0.0312 | 0.2388 | 0.8113 | 95% | Random | Not apparent |
| Getis-Ord General G-Index | 33 | 0.4627 | 0.4734 | -1.1252 | 0.2605 | 95% | Random | Not apparent |
| | | Observed General G | Expected General G | | | | | |

APPENDIX II: FIGURES

Figure 1. Map of the eastern South Pacific region. The study area was located on the Coast of Esmeraldas (Bajos de Atacames), Ecuador.

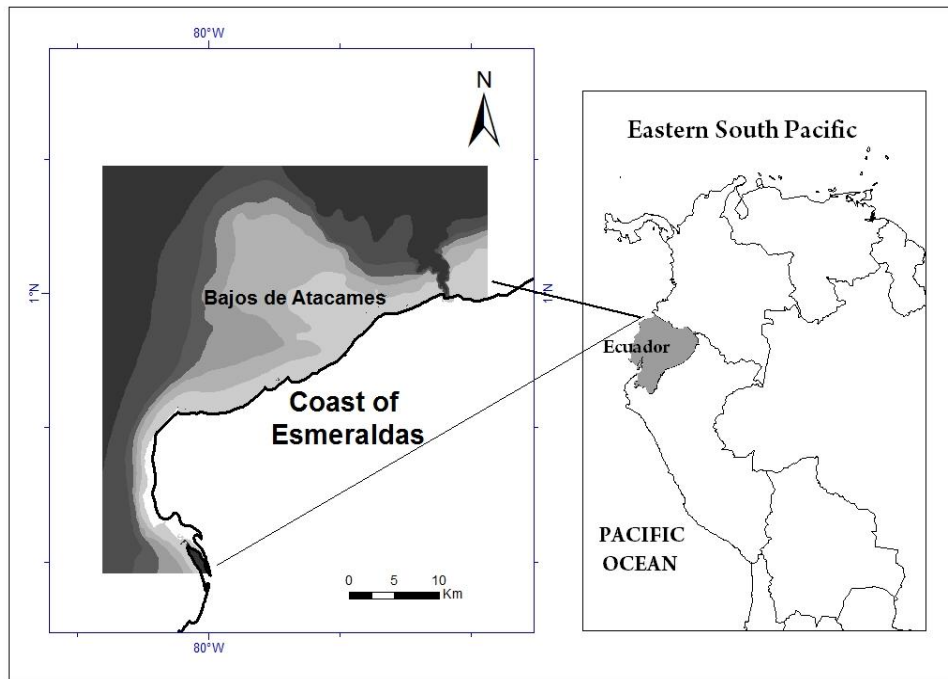


Figure 2. Humpback whales survey effort from 2012 (June to August) over bathymetry off the coast of Esmeraldas.

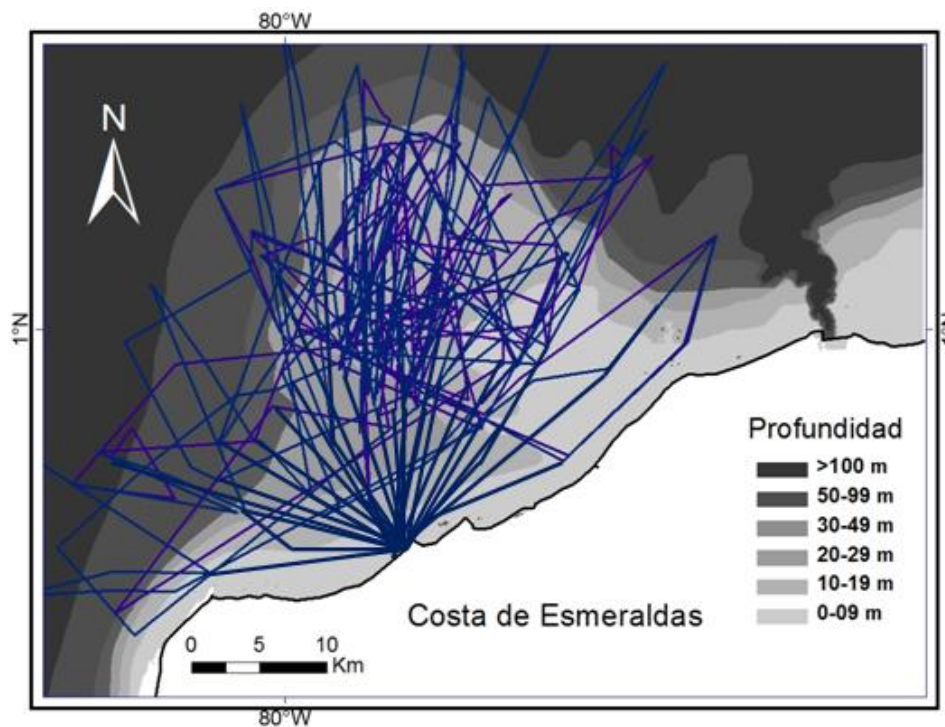


Figure 3. Humpback whale social group distribution according to geographic bathymetry and bottom composition.

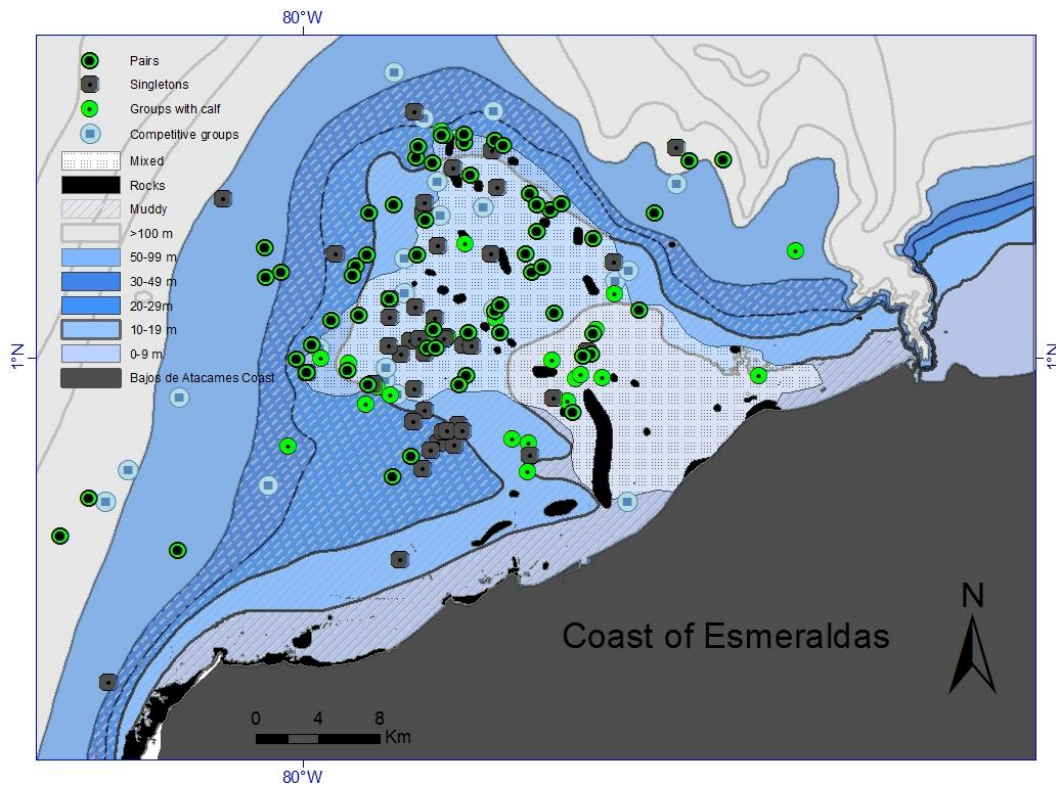


Figure 4. Frequency spectrogram from recordings of very good and very poor song quality.

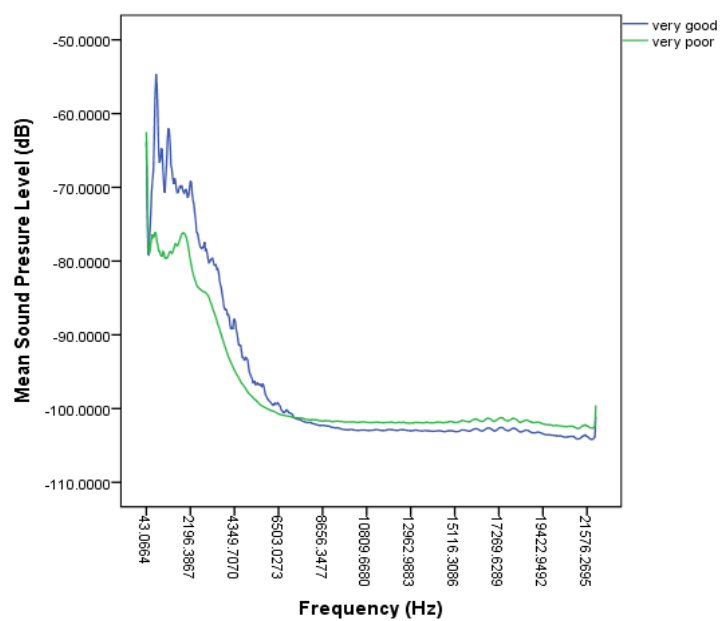


Figure 5. Social groups of humpback whales and percentage in Bajos de Atacames.

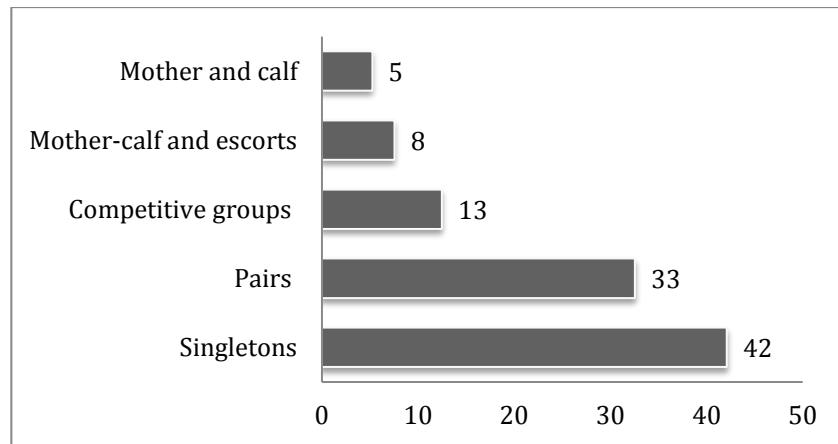


Figure 6. Percentage of sightings of every humpback whale social group among depths. (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

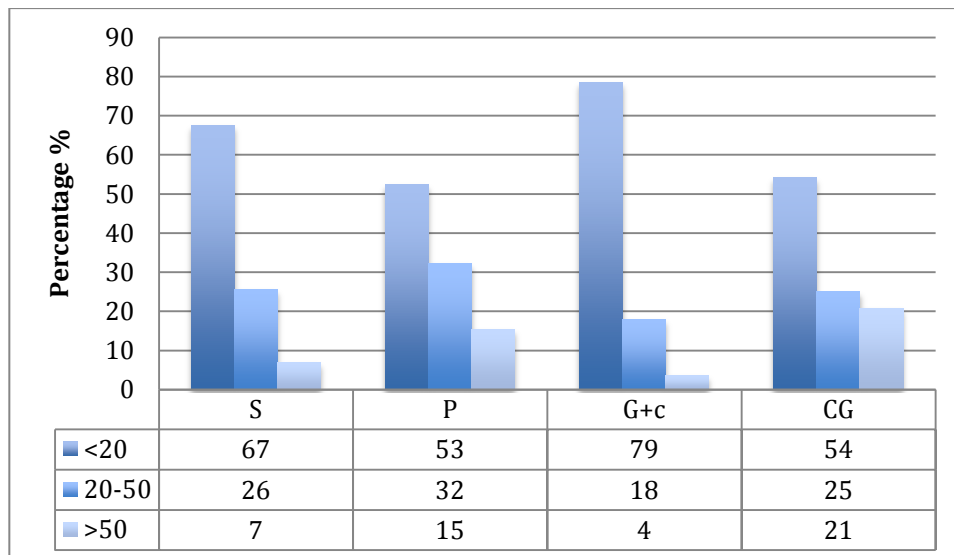


Figure 7. Percentage of sightings of every humpback whale social group between bottom type. (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups).

Columns presented sum to 100%.

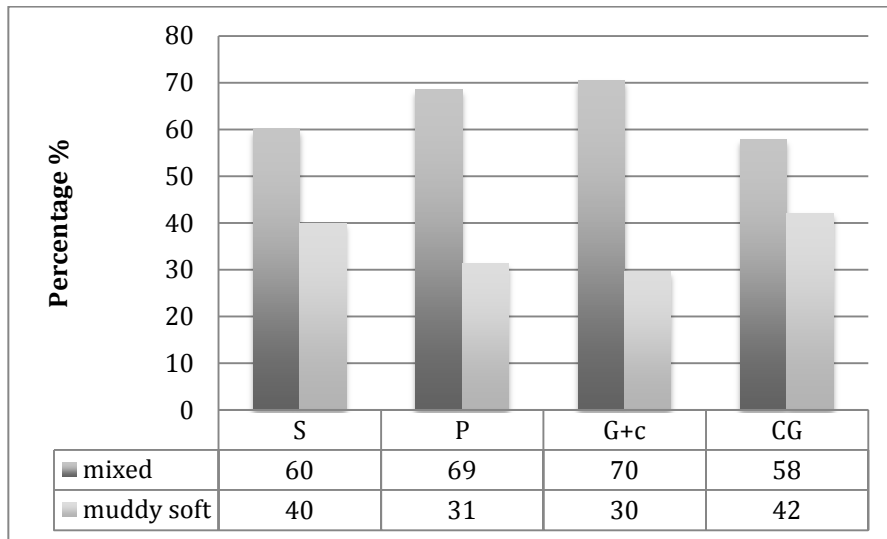


Figure 8. Percentage of sightings for all humpback whale social groups by depth.

(S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

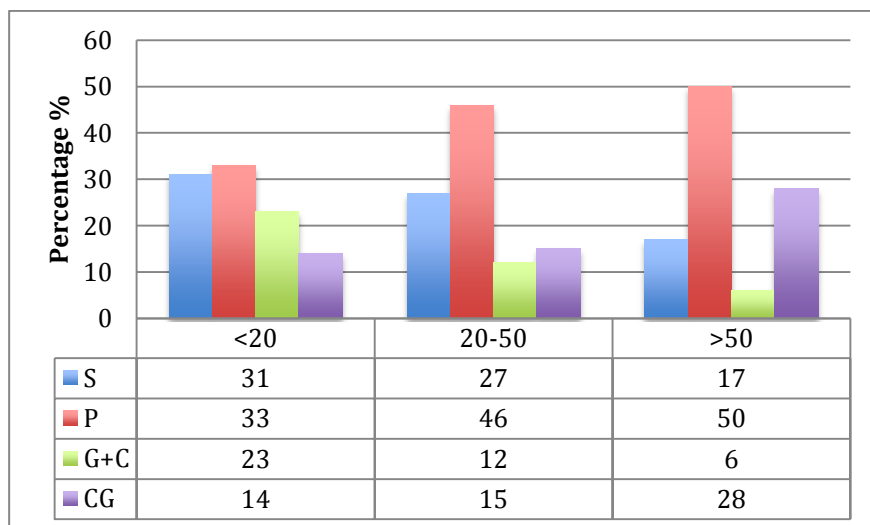


Figure 9. Percentage of sightings for all humpback whale social groups by substrate type (S = Singletons; P = Pairs; G+c = Groups with calf; CG = Competitive groups). Columns presented sum to 100%.

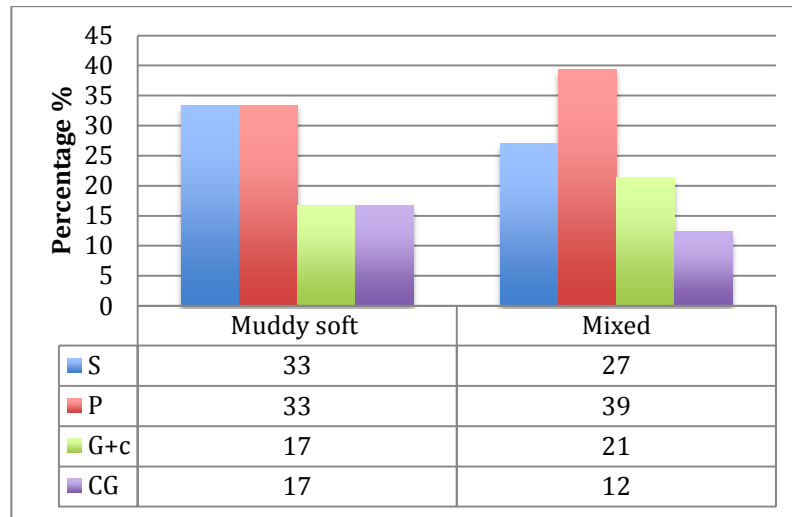


Figure 10. Ripley's K-Function of the overall humpback whale distribution off Esmeraldas during 2012. The observed K-function is higher than the expected indicating a clustered distribution.

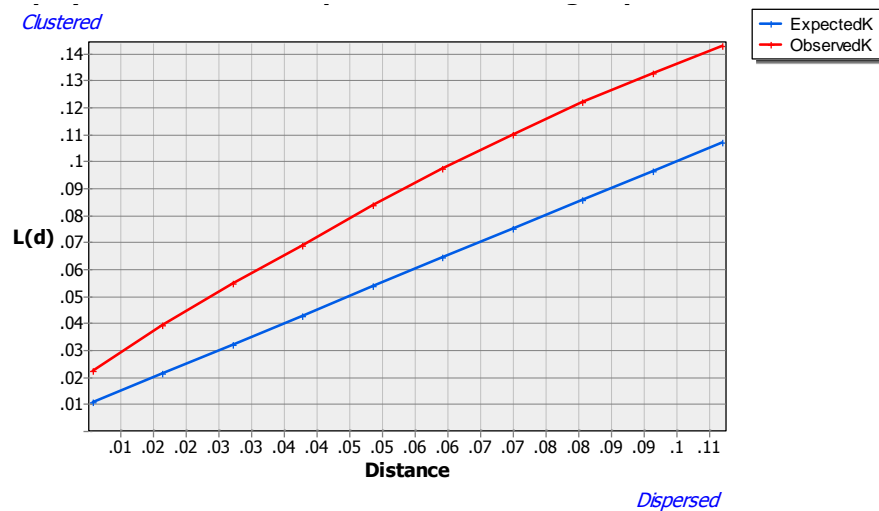


Figure 11. Occurrence of humpback whale song based on depth (0 to > 100 m) and bottom composition (mixed/muddy soft). Level of song very good (2 km) and good (5 km) are presented with buffers where potentially singers were singing.

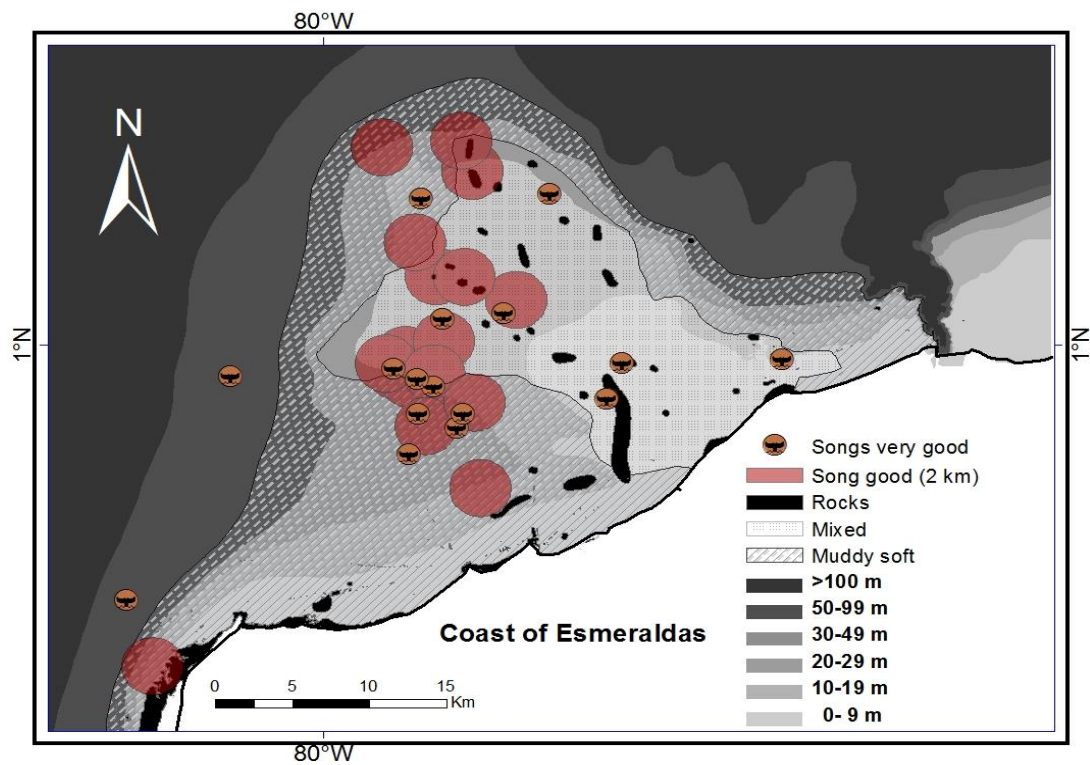


Figure 12. Behavior and social groups during acoustic surveys: traveling, pectorial slapping, tail slapping, breaching, mother-calf and pairs.

