

# A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador

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## ABSTRACT

A photo-identification study of humpback whales (*Megaptera novaeangliae*) was conducted between 1996 and 1999 in the Machalilla National Park off mainland Ecuador. This paper compares the results obtained with those from known breeding grounds for humpback whales to determine whether the area represents a breeding area for this species. Factors considered included: seasonality in abundance; population structure (including cow-calf pairs and escort whales) in the breeding area; presence of singers; and occupancy and residence times. It is concluded that the area does represent a breeding ground but the relationship of the animals using this area with those using other areas of the eastern tropical Pacific (and the Antarctic feeding grounds) requires further work. The paper also presents a preliminary estimate of abundance (405, 95%CI 221-531) for the years 1998/1999 using the Chapman-modified Peterson method.

KEYWORDS: HUMPBACK WHALE; SOUTH AMERICA; PACIFIC OCEAN; BREEDING GROUNDS; PHOTO-ID, MARK-RECAPTURE; SITE FIDELITY

## INTRODUCTION

Southern Hemisphere humpback whales (*Megaptera novaeangliae*) migrate from their feeding grounds in Antarctic waters to the tropics where they reproduce in the austral winter (Matthews, 1937). On the breeding grounds, humpback whales mate, calve and feed little or not at all (e.g. Chittleborough, 1965). Mackintosh (1942; 1965) recognised six stocks distributed around the Antarctic continent during the austral summer. During the winter, each stock migrates towards the Equator to its own coastal or insular breeding ground in tropical or near-tropical waters. Known breeding grounds in the Southern Hemisphere are found off Africa (Rosenbaum *et al.*, 1997), Australia (Chittleborough, 1965), the southern Pacific islands (Dawbin, 1966; Hauser *et al.*, 2000) and South America (Winn and Reichley, 1985). The most recent review of Southern Hemisphere humpback whale feeding and breeding grounds is given in IWC (2001). There is little information available on the distribution of reproductive areas or on the movement of humpback whales in the eastern tropical Pacific. Such information is essential for determining the abundance of this particular stock and to monitor any possible recovery of the species, as has been documented elsewhere (e.g. see IWC, 2001).

The only well known reproductive area for humpback whales in the eastern tropical Pacific is around the Gorgona Islands in Colombia. Estimates for this population range between 170-450 animals (Flórez-González, 1991) and re-sightings with Antarctic humpbacks have confirmed that these animals migrate from Antarctic waters (Stone *et al.*, 1990). Humpback whales have also been sighted around Coco Island in Costa Rica (Acevedo and Smultea, 1995), Panama (Flórez-González *et al.*, 1998) and the Galapagos Islands (Merlen, pers. comm.), although it is not known whether these areas are used for reproduction.

Humpback whales are sighted off the Ecuadorian mainland in the marine area of the Machalilla National Park from June to September (Scheidat *et al.*, 1997). Within the last five years, a small whalewatching industry has

developed in the fishing village of Puerto Lopez. Flórez-González *et al.* (1998) suggested that the humpback whales seen off the Ecuadorian coast only pass through the area while migrating to Colombia or possibly use the whole eastern tropical Pacific as a wintering ground, rather than being confined to a specific breeding site off Ecuador.

Humpback whale reproductive areas are characterised by certain oceanographic features, such as shallow waters with preferably banks of less than 60m (Whitehead and Moore, 1982). The water temperatures of humpback whale breeding grounds range from the coldest waters of 19-20°C in the Bonin Islands (Japan) to the warmer temperatures of 24-28°C in the West Indies (Naughton, 1997). In such areas, humpback whales exhibit behaviour associated with reproduction, such as aggression between males that compete for sexually mature females (Baker and Herman, 1984) and the presentation of typical 'songs' (Tyack, 1981). Young calves are also observed at such sites. The primary aim of this paper is to determine if the area of the Machalilla National Park is a breeding ground for the humpback whales of the South Pacific.

## METHODS

### Study area

The study area is a large bight on the continental shelf approximately 25 n.miles long and 20 n.miles wide. The maximum depth is 200m, with shallow areas of 10-30m around the Isla de la Plata, the Cantagallo shallow and along the coast. The sea bottom consists of sand, rocky areas and coral reefs (Ayón, 1988). The Isla de la Plata, as well as the area of the Cantagallo shallow, is characterised by sand and coral reefs (Anon., 1997). Beyond Isla de la Plata the continental shelf drops away rapidly to depths of more than 3,000m (Fig. 1).

The study area is influenced by several large current systems. During the dry season (June to September), the Ecuadorian Countercurrent comes from the west between 4° and 10° north and is deflected by the continent where it splits

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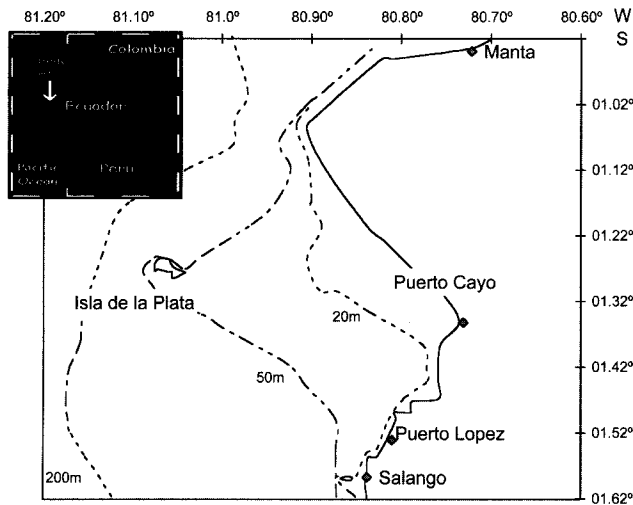


Fig. 1. Map of the study area.

into the North Ecuadorial Current and the South Ecuadorial Current. The Humboldt Current from the south, forms the Ecuadorial Front when it meets the South Ecuadorial Current. During the dry season this front lies in the study area between 1° and 5° south and is characterised by high quantities of nutrients (Anon., 1997). These waters have high zooplankton and fish densities and support a local fishing industry, suggesting that the bay exhibits a level of primary productivity that is atypically high among tropical marine systems (Anon., 1997). Prevailing winds are southwesterly trade winds.

### Data collection

Humpback whales can be individually identified by unique features in the coloration, shape and scarring pattern of the ventral side of their flukes (Katona and Whitehead, 1981). Photos of humpback whale flukes were taken in the study area during the austral summer from 1996 to 1999. Within any season, whenever possible, daily trips were undertaken for the purpose of photo-identification. Effort in 1996 concentrated on the months of August and September, with a total of 28 boat trips conducted. In 1997, the field season did not start before late-July and ended in September and 36 trips were made. In 1998 and 1999, sampling took place from June-September with 40 and 42 trips, respectively. For the analyses of group composition only the year 1999 was used, as oceanographic conditions made 1997 and 1998 atypical years (see Discussion).

For analyses of relative abundance, behaviour and group sizes, only the 1999 data were used. In 1999, effort took place from 10 June to 18 September, covering the widest time period available to this study and thus potentially giving a better idea of the migration pattern of the whales.

Photo-identification was carried out from whalewatching vessels leaving from Puerto Lopez or Puerto Cayo travelling to the Isla de la Plata. The boats were 6-8m long with 75 or 115hp engines. Photos were taken from the roofs of the vessels at a height of about 2m with a 35mm single-lens reflex camera equipped with either a 300mm lens or 70-210mm zoom lens and using 200 ASA colour slide film.

For each sighting of a whale or group of whales, the time, GPS position, behaviour, group composition, group size and the pictures taken from each animal were recorded. In the later analyses, all fluke photographs were judged to be of either good, fair or poor quality. Good and fair quality

photographs showed at least 50% of the fluke at an angle sufficiently vertical to distinguish the shape of the flukes' trailing edges. For this study, poor-quality photographs were deleted from the dataset. The best photograph of a fluke taken during one sighting was assigned an identification number. During the matching of fluke photographs, a whale that was identified on more than one occasion was assigned an animal number, allowing us to reference all fluke identifications of that individual. All fluke photographs of good or fair quality were scanned with a slide scanner and stored in a data file together with the additional information available for that sighting.

To estimate population size in the Machalilla National Park, Chapman's modification of the Petersen method for closed populations was used (Seber, 1973). The 95% Confidence Interval was approximated according to Sutherland (1996). The main assumptions underlying Petersen's method are: (1) the population is closed, i.e. no whales leave or enter the population before the second sample; (2) during a sampling period all whales have the same probability of being sighted, photographed and identified; and (3) fluke patterns do not change between sample periods and each pattern can be identified. The general applicability of these assumptions to photo-identification data have been discussed extensively elsewhere (e.g. Hammond, 1986). An open population model such as the Jolly-Seber model was not used because a small sample size can lead to high variability and imprecision.

A hydrophone was deployed on a total of 12 occasions to listen for humpback whales. As the study was conducted from whalewatching vessels, individual whales could not be followed for identification or their position determined.

### Definitions

#### *Relative abundance*

This was defined as the number of whales per hour searched by the whalewatching vessel. The search effort only includes the time actively searched by the researcher and does not include the time spent with a sighting.

#### *Sighting*

A sighting was defined as either a lone whale, or a group of whales where members of the group were within 100m of each other and generally moving in the same direction and coordinating their behaviour (Mobley and Herman, 1985).

#### *Calf*

A calf was defined as an animal in close proximity to another whale (less than one whale length separating the pair), and estimated to be less than 50% of the length of the accompanying animal.

#### *Occupancy*

Occupancy was estimated as the period, in days, between the first and last sighting of a whale in a season.

#### *Surface active behaviour*

All surface active behaviour, agonistic behaviour and possible breeding behaviour was pooled together into one category. Surface active behaviour included breaches as well as flipper or fluke slapping and waving. Agonistic behaviour included head lunges, breaches, fluke and flipper-slaps that were directed towards another whale (Tyack and Whitehead, 1983; Baker and Herman, 1984; Winn and Reichley, 1985).

Behaviour thought to be associated with breeding was defined as belly flipping, rolling or 'headstands' (Tyack, 1981).

## RESULTS

### Relative abundance

In 1999, whalewatching operators observed the first humpback whales on 16 May. The relative abundance calculated from the transects varied from a minimum average of 0.3 animals/hour on 17 June to the maximum of 7.2 animals/hour on 23 July. Fig. 2 shows an increase in whale abundance in mid/late June and a decrease of abundance at the beginning of September.

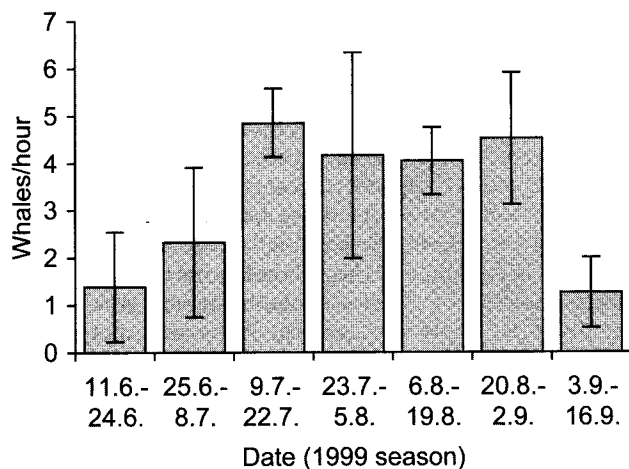


Fig. 2. Seasonal changes in relative abundance of humpback whales throughout the 1999 season. Relative abundance is represented by the average number of whales seen per hour in each two-week period (error bars represent SD).

### Group size

In 1999, a total of 109 sightings was made (254 whales), with the mean group size being 2.33 (SD = 1.05). The modal pod size was two. Pod sizes varied between one and a maximum of eight animals. Mean group size increased from 2.11 in early season (10 June to 8 July), to 2.29 in mid-season (9 July to 19 August) and to 2.46 in late season (20 August to 18 September) (Fig. 3). The differences between the distribution of group sizes from early, mid- and late season were not significant ( $\chi^2$  - test:  $p > 0.1$ ).

### Presence of calves

The first calf sighting during this study was made on 22 July 1999. On 5 August 1999, a calf was observed that was estimated to be less < 5m in length and which had a dorsal fin that was doubled over, indicating a recent birth. In July 1995, the captain of the National Park vessel had observed the birth of a humpback whale calf close to the Isla de la Plata (R. Gonzalez, pers. comm.). In 1998, a humpback whale calf was caught by a fisherman close to the coast (at about 80°49'W and 01°24'S). It could not be determined whether the calf was already dead when caught or had died in the net.

The percentage of humpback whale sightings that included a calf increased from 7% in mid-season (9 July to 19 August) to 17% in late season (20 August to 18 September) (Fig. 3).

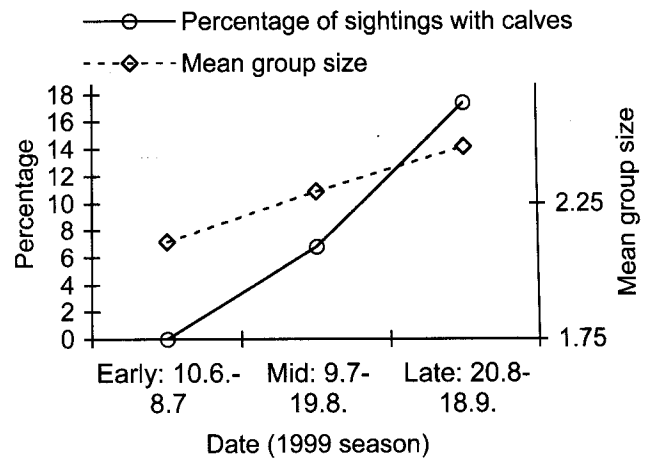


Fig. 3. Seasonal changes in mean group size and percentage of sightings with calves in the 1999 season.

For pods with calves, a group of two signifies a mother-calf pair alone. Larger-sized pods indicate that other adult whales known as 'escorts' (Herman and Antinofa, 1977) were accompanying the mother-calf pair. It was more common for a mother-calf pair to be seen in the company of other whales than to be seen alone and 61.5% of all sightings consisted of three or more animals.

Of all sightings with calves, the most common comprised triads of the mother, calf and an accompanying escort (46.1%); 15.4% were part of a group of whales of more than two adults and 38.5% were mother-calf pairs. Throughout the season the group size of pods with calves increased. During the two-week period from 6-19 August, all mother-calf pairs were accompanied by at least one other adult whale.

### Surface active behaviour

Throughout the season, breaching as well as fluke and flipper slapping was observed. 'Tail breaches' used against other animals were seen on numerous occasions. Here, the rear third of the body was thrown out of the water and slammed sideways and downwards against the water surface. Fluke slaps and head lunges from one whale directed towards another and animals exhaling under water and creating bubbles, vocalising above the water ('trumpet blows') and breaching were also seen, as well as flipper slapping in close proximity to other whales. Other behaviours included belly flipping, spyhops, rolling and 'headstands'. On one occasion a humpback whale stayed in the 'headstand' position for up to 17 minutes before returning briefly to a horizontal position to breathe. A second whale in close proximity was observed to stay underwater, apparently pushing its head against the ventral side of the whale executing the headstand. This behaviour was observed from the shore continuously for three hours with the whale only returning to the horizontal position to breathe. The sex of the individual whales could not be determined.

Throughout the season the frequency of surface active behaviour increased. In the two-week period from 23 June to 5 August 1999, 67% of the sightings contained individuals that were engaged in surface active behaviour (Fig. 4). Towards the end of the season this percentage decreased to 38%.

On ten of the twelve occasions when a hydrophone was deployed, humpback whale songs could be heard.

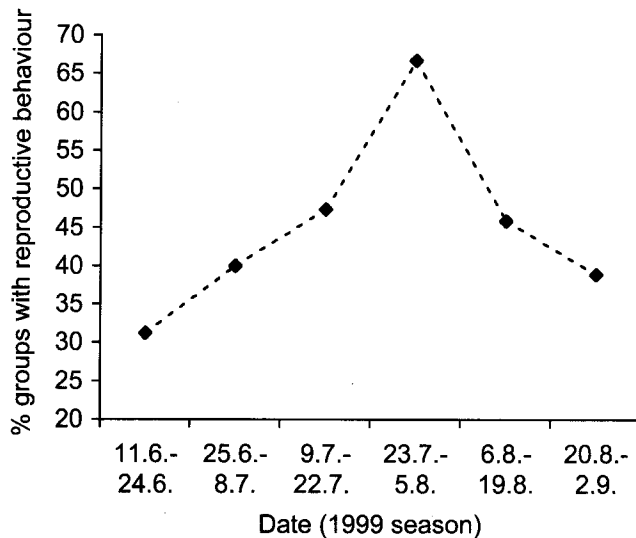


Fig. 4. Seasonal changes in frequency of surface active behaviour during 1999.

Table 1  
Sighting history of individual whales seen between 1996 and 1999.

Whale ID	1996	1997	1998	1999
C96-8	X	X		
C96-10	X			X
C96-13	X		X	
C97-4		X	X	
C97-12	X	X	X	X

#### Annual return

Table 1 shows the number of animals that were identified individually. In total, fluke pictures of 209 individuals were taken. Of these, 116 were poor quality and were not considered in the analyses. A total of 93 different individual humpback whales was identified during the study years 1996 to 1999 using fluke identification. Of these, five different animals were re-sighted between years.

#### Within-season occupancy

Table 2 summarises data on effort and on occupancy of individual whales during the period 1996 to 1999. Observed occupancy of individuals ranged from 1 to 30 days; the mean occupancy for all whales observed in a year varied from 7-21.67 days, with an overall mean of 13 days. A total of 12 different whales were seen more than once in a year. In 1997, one individual humpback whale was first photographed on 26 August, then again on 31 August, 23 September and 24 September.

Table 2  
Number of cruises made, maximum and mean occupancy (in days) of individuals for each year.

	1996	1997	1998	1999	All years
No. of cruises	28	36	40	42	146
Occupancy					
Mean	12.00	12.33	21.67	7	13
Maximum	28	29	30	17	30
SD	14.00	14.43	7.37	8.66	11.3

Table 3

Calculated population estimates using the Chapman's modified Petersen estimator (no replacement) between years.

	$n_1$	$n_2$	$m_i$	$N$	95% CI
1996-1997	29	14	2	149	80 - 380
1997-1998	14	28	2	144	78 - 385
1998-1999	28	27	1	405	221 - 531

#### Population estimate

Population size was calculated between years (Table 3) with Chapman's modified estimator for the Petersen model. Population estimates varied between 144 to 405 animals.

#### DISCUSSION

##### Evidence that the Machalilla National Park represents a breeding area

###### Seasonality in abundance

The relative abundance of humpback whales in the study area shows a typical breeding ground pattern - increasing relative abundance after the arrival of humpback whales in June, a peak in relative abundance from July to August and decreasing relative abundance with the onset of the southern migration in September. This is similar, for example, to the pattern observed for North Atlantic humpback whales (e.g. Mattila *et al.*, 1994). By contrast, if the area was merely along a migration route, one would expect to see a bimodal distribution with higher number of whales during the migration periods of June and September. This has been observed in other areas such as the west coast of South Africa (Best *et al.*, 1995) and off Brisbane in Australia, where peaks of abundance are found during the northward migration from June to July as well as during the southward migration from August to the end of October (Bryden *et al.*, 1990).

###### Population structure in the breeding area

Whaling data from the South Pacific suggest that the majority of the sexually mature males migrate toward the lower latitudes after the immature animals and late-pregnant females, arriving at the wintering grounds in late July. Non-pregnant females closely follow the mature males; presumably, these females make up the majority of that season's female breeding population (Chittleborough, 1958; Dawbin, 1997). Female humpback whales have their calves in the winter and, since the gestation period is about one year, mating must therefore occur during the same season (e.g. Mackintosh, 1942; 1965).

In the present study, about 60% of the sightings with calves were mother-calf pairs that were accompanied by one or more adult whales. A similar percentage was found by Mobley and Herman (1985) in the Hawaiian breeding grounds. By the beginning of August, the group size of sightings with calves increased to a modal group size of three. The escorts of mother-calf pairs are thought to be males seeking access to reproductively active females (Tyack, 1981; Clapham *et al.*, 1992), although the probability of post-partum ovulation leading to successful conception may not be high (Glockner-Ferrari and Ferrari, 1984; Corkeron *et al.*, 1994). The presence of adults whales around a new-born calf might also help to protect against attacks from killer whales (*Orcinus orca*). The authors observed such an attack in July 1997, when two adult male killer whales attacked a group of five humpback whales, one of them a calf, close to the Isla de la Plata. The calf showed

an injury on its fluke but appears to have survived. Such attacks have also been observed in the Colombian breeding ground (Flórez-González *et al.*, 1994).

### Behaviour

The mean group size of humpback whale sightings increased from the end of July to the beginning of September, although this was not statistically significant. Such an increase can be explained in part by the presence of calves but also by the formation of competitive groups. Competitive groups and their behaviour were first described in detail by Tyack and Whitehead (1983) as well as by Baker and Herman (1984), who suggested that such groups consist of several adult males competing for sexual access to a single mature female. A variety of agonistic behaviour was observed which has been described in detail for humpback whales while in their breeding grounds (Tyack, 1981; Winn and Reichley, 1985; Clapham *et al.*, 1992).

### Presence of singers

Humpback whale songs are a distinctive continuous sequence of vocalisations generally performed by males (Whitehead, 1985). Singing is almost never heard on the feeding grounds (Perkins and Whitehead, 1977; Clapham *et al.*, 1992) and research by Tyack (1981) off Hawaii relates singing to mate attraction; Frankel *et al.* (1995) suggest that the songs are a spacing mechanism between males. Although systematic acoustic research could not be conducted, the presence of songs does indicate that the study area is a reproduction ground.

### Resightings

Five individuals were re-sighted between years and one animal was seen every year from 1996. Not only did individual humpbacks return to the study area, but re-sightings were also made within a given season. The maximum occupancy time observed in the study area was 30 days. However, not all pods in the study area were sampled every day and sample sizes are inevitably small. The estimates presented here can probably be considered as minimum times. The available data suggest that most whales spend a short period (up to five days) in the area, but around 10% spend more than two weeks in the study area. It may be that some whales established preferred ranges within the study area while others were relatively transient.

The occupancy times found for the Machalilla National Park are similar to those found in known reproductive areas. For example, in a study on Silver Bank (West Indies), where 9.1% of identified whales were sighted again in the same season, the greatest time between first and last sighting was 30 days and the mean period of residency of the whales was 8.52 days (Mattila *et al.*, 1989). The longest sighting interval reported by Baker and Herman (1981) was 44 days where an animal was first seen in Hawaii and then in Maui (a relatively long movement). They also reported resightings of a mother-calf pair over a 26 day period and whales were re-photographed at periods ranging from a few days to as long as 34 days. A study in Samana Bay, Dominican Republic (Mattila *et al.*, 1994), showed the largest time interval between identified whales within a season to be 33 days.

### Relationship with other areas in the eastern tropical Pacific

Some humpback whales have been documented moving between breeding grounds, for example within the West Indies (Mattila *et al.*, 1994), between Hawaii and Mexico

(Darling and Jurasz, 1983) and between Hawaii and Japan (Salden *et al.*, 1999). Salden *et al.* (1999) suggest that these wanderers are mainly males. Nevertheless, movement between wintering grounds is relatively rare compared to regional return (e.g. Baker *et al.*, 1985). However, within a larger reproductive area, such as the Hawaiian Islands, extensive movement of individuals does take place. Cerchio *et al.* (1998) showed that individual humpbacks, mostly males, can move between the Hawaiian islands of Kauai and Hawaii over short time periods. In the eastern tropical Pacific one humpback whale has been sighted in Colombia and Ecuador, but not in the same year (Flórez-González *et al.*, 1998). The distance between the Machalilla National Park and Gorgona Island is about 325 n.miles and could be travelled in about 10 days, at a speed of 220 n.miles per week (Dawbin, 1966). Therefore, it is possible that the Ecuadorian and Colombian humpback whales are part of a larger reproductive area in which some movement takes place.

Bravo *et al.* (1994) noted that humpback whales have been observed as early as mid-June in the Colombian breeding ground, with peak abundance between August and October and some seen as late as mid-December. If the Colombian humpback 'population' arrives in June in Colombia this could mean that at least part of the it passes through the Machalilla National Park during their northbound migration. A strong peak in relative abundance is apparent at the beginning of July, possibly indicating an overlap of these 'populations'. The season off the Ecuadorian coast is from mid-May to mid-October, with humpback whales rarely being sighted after the beginning of October, even though whalewatching tours go to the Isla de la Plata throughout the year and record sightings of cetaceans outside of the typical humpback whale season. It is therefore improbable that the whales from the Colombian population pass through the Machalilla National Park on their southward migration.

One possible scenario is that at the end of the reproductive season, the humpback whales off Colombia move west before starting south, possibly passing the Galapagos Islands where humpback whales are sighted from July to September. However, only a few individuals are observed there and no increase of sightings by month is apparent (G. Merlen, pers. comm.). Further research, to include the islands of Coco, Galapagos and the waters of Panama, is needed to understand the migration patterns of the humpback whales present in this area.

### Preliminary abundance estimate

Mark-recapture models make a number of assumptions (e.g. see Hammond, 1986; Hammond *et al.*, 1990). The point estimates presented here for the Chapman-modified Petersen (closed population) model vary between 144 and 405 animals. One of main assumptions is that all animals have an equal capture probability. In 1997, only 12 new animals could be identified by their flukes, although the effort was as high as in other years (Table 1). The sea surface temperature in the Machalilla National Park during the dry season from April to September typically lies between 20°C and 24°C (Stevenson *et al.*, 1970). In 1997, due to the El Niño Southern Oscillation, sea surface temperatures in the study area were up to 10°C higher than in 'normal' years, taking local surface temperatures in 1997 up to 30°C (CPPS, 1999). It seems that either fewer humpback whales were present or that the animals changed their behaviour in a way that made them harder to see and photograph. A thorough analysis of the possible effect of El Niño will be the subject of a future paper. Given the problems with the 1997 data, we believe that the estimate of 405 animals (95%CI 221-531) for the

years 1998 to 1999 represents the best preliminary abundance estimate for the humpback whale population in non-El Niño years. It should be noted that estimating population size from mark-recapture studied in breeding areas alone will generally result in a negatively biased estimate due to heterogeneity in capture probabilities arising out of differences in sex/reproductive class (Smith *et al.*, 1999). Future combination of Antarctic catalogues as well as increased effort in Ecuadorian waters should provide a better estimate in the future.

## CONCLUSION

The increase in reproductive behaviour and the observation of young calves, as well as the increase in relative abundance throughout the season and re-sightings of individual animals over several years, provides evidence that the area of the Machalilla National Park forms a reproductive area for humpback whales. However, data are lacking to determine if the area represents a distinct breeding ground or rather a preferred habitat for humpback whales that use a larger seasonal range in the eastern tropical Pacific. A comparison of the photo-identification catalogues of the different research sites in the eastern tropical Pacific as well as in the Antarctic feeding grounds is needed to increase our understanding of the migration routes and the distribution of breeding grounds. Genetic studies and song comparison should help clarify the stock identity of these humpback whales.

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## REFERENCES

- Acevedo, A. and Smultea, M.A. 1995. First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemisphere populations. *Mar. Mammal Sci.* 11(4):554-60.
- Anonymous. 1997. *Evaluación del Área Marina del Parque Nacional Machalilla*. Parts 1 and 2. Instituto Ecuatoriano Forestal y de Áreas Naturales y Vida Silvestre (INEFAN) and Dirección Nacional de Áreas Naturales y Vida Silvestre (DNANVS). 97pp. [In Spanish]. [Available from Parque Nacional Machalilla, Pto. Lopez, Ecuador].
- Ayón, H. 1988. *Grandes Rasgos Geomorfológicos de la Costa Ecuatoriana*. PMRC (Programa del Manejo de Recursos Costeros), Ecuador. 128pp. [In Spanish]. [Available from [www.pmr.org.ec](http://www.pmr.org.ec)].
- Baker, C.S. and Herman, L.M. 1981. Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Can. J. Zool.* 59:460-9.
- Baker, C.S. and Herman, L.M. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Can. J. Zool.* 62:1922-37.
- Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M. and Straley, J.H. 1985. Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Mar. Mammal Sci.* 1(4):304-23.
- Best, P.B., Sekiguchi, K. and Findlay, K.P. 1995. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Mar. Ecol. Prog. Ser.* 118(1-3):1-12.
- Bravo, G.A., Flórez-González, L. and Capella, A. 1994. Natalidad y frecuencia estacional de crías de Ballena Jorobada, *Megaptera novaeangliae*, en el Pacífico Colombiano. Paper presented at the Anais da 6ª Reunião de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul. Florianópolis-Brasil, (unpublished). 76pp. [In Spanish]. [Available from Fundación Yubarta, [lilianfg@biomarina.univalle.edu.co](mailto:lilianfg@biomarina.univalle.edu.co)].
- Bryden, M.M., Kirkwood, G.P. and Slade, R.W. 1990. Humpback whales, Area V. An increase in numbers off Australia's east coast. pp. 261-77. In: K.R. Kerry and G. Hempel (eds.) *Antarctic Ecosystems. Ecological Change and Conservation*. Springer-Verlag, Berlin, Heidelberg. 327pp.
- Cerchio, S., Gabriele, C.M., Norris, T.F. and Herman, L.M. 1998. Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. *Mar. Ecol. Prog. Ser.* 175:13-22.
- Chittleborough, R.G. 1958. Dynamics of two populations of the humpback whales *Megaptera nodosa* (Bonnaterre). *Aust. J. Mar. Freshwater Res.* 9:1-29.
- Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16:33-128.
- Clapham, P.J., Palsbøll, P.J., Mattila, D.K. and Vasquez, O. 1992. Composition and dynamics of humpback whale competitive groups in the West-Indies. *Behaviour* 122(Part 3-4):182-94.
- Corkeron, P.J., Brown, M., Slade, R.W. and Bryden, M.M. 1994. Humpback whales, *Megaptera novaeangliae* (Cetacea: Balaenopteridae), in Hervey Bay, Queensland. *Wildl. Res.* 21:293-305.
- CPPS. 1999. XII reunion del comité científico del programa ERFEN. Guayaquil, Ecuador, 2, 3 and 4 November 1998. Final report to the Comisión Permanente de Pacífico Sur. 151pp. [In Spanish]. [Available from [www.cpps.org.ec](http://www.cpps.org.ec)].
- Darling, J.D. and Jurasz, C.M. 1983. Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). pp. 359-68. In: R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposium 76. Westview Press, Colorado. xii+643pp.
- Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp. 145-70. In: K.S. Norris (ed.) *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles. xv+789pp.
- Dawbin, W.H. 1997. Temporal segregation of humpback whales during migration in Southern Hemisphere waters. *Mem. Queensl. Mus.* 42(1):105-38.
- Flórez-González, L. 1991. Humpback whales, *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. *Mem. Queensl. Mus.* 30(2):291-5.
- Flórez-González, L., Capella, J.J. and Rosenbaum, H.C. 1994. Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. *Mar. Mammal Sci.* 10(2):218-22.
- Flórez-González, L., Capella, J., Haase, B., Bravo, G.A., Felix, F. and Gerrodette, T. 1998. Changes in winter destinations and the northernmost record of southeastern Pacific humpback whales. *Mar. Mammal Sci.* 14(1):189-96.
- Frankel, A.S., Clark, C.W., Herman, L.M. and Gabriele, C.M. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. *Can. J. Zool.* 73:1,134-46.
- Glockner-Ferrari, D.A. and Ferrari, M.J. 1984. Reproduction in humpback whales, *Megaptera novaeangliae*, in Hawaiian waters. *Rep. int. Whal. Commn* (special issue) 6:237-42.
- Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn* (special issue) 8:253-82.
- Hammond, P.S., Mizroch, S.A. and Donovan, G.P. (eds.). 1990. *Report of the International Whaling Commission (Special Issue 12). Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge, UK. [vi]+440pp.
- Hauser, N., Peckham, H. and Clapham, P. 2000. Humpback whales in the Southern Cook Islands, South Pacific. *J. Cetacean Res. Manage.* 2(3):159-64.
- Herman, L.M. and Antinaja, R.C. 1977. Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst., Tokyo* 29:59-85.

- International Whaling Commission. 2001. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 3:In press.
- Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20:439-44.
- Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22:197-300.
- Mackintosh, N.A. 1965. *The Stocks of Whales*. Fishing News (Books) Ltd, London. 232pp.
- Matthews, L.H. 1937. The humpback whale, *Megaptera nodosa*. *Discovery Rep.* 17:7-92.
- Mattila, D.K., Clapham, P.J., Katona, S.K. and Stone, G.S. 1989. Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. *Can. J. Zool.* 67:281-5.
- Mattila, D.K., Clapham, P.J., Vasquez, O. and Bowman, R.S. 1994. Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. *Can. J. Zool.* 72(11):1898-907.
- Mobley, J.R. and Herman, L.M. 1985. Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Can. J. Zool.* 63:762-72.
- Naughton, J.J. 1997. Winter breeding habitat characteristics of the humpback whale. pp. 56-9. In: R. Payne, P. Micheal, B. Philips and E.T.C. Nitta (eds.) *Report of the Workshop to Assess Research and Other Needs and Opportunities Related to Humpback Whale Management in the Hawaiian Islands, 26-28 April 1995, Kaanapali, Maui, Hawaii*. US Department of Commerce, NOAA Technical Memorandum NMFS-OPR-11, [Available from <http://www.ntis.gov>].
- Perkins, J. and Whitehead, H. 1977. Observations on the three species of baleen whales off northern Newfoundland and adjacent waters. *J. Fish. Res. Bd Can.* 34(9):1436-40.
- Rosenbaum, H.C., Walsh, P.D., Razafindrakoto, Y., Vely, M. and DeSalle, R. 1997. First description of a humpback whale breeding ground in Baie d'Antongil, Madagascar. *Conserv. Biol.* 11(2):312-4.
- Salden, D.R., Herman, L.M., Yamaguchi, M. and Sato, F. 1999. Multiple visits of individual humpback whales (*Megaptera novaeangliae*) between the Hawaiian and Japanese winter grounds. *Can. J. Zool.* 77:504-8.
- Scheidat, M., Denking, J. and Pairoa Riofrio, C. 1997. Preliminary results of a study on the habitat use of humpback whales (*Megaptera novaeangliae*) in the Machalilla National Park, Ecuador. Paper presented at the Eleventh Annual Conference of the European Cetacean Society, Stralsund, 10-12 March 1997, (unpublished). 3pp. [Available from [mscheidat@aol.com](mailto:mscheidat@aol.com)].
- Seber, G.A.F. 1973. *The Estimation of Animal Abundance*. Hafner Publ. Co., Inc., New York. 506pp.
- Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Mattila, D., Palsbøll, P.J., Sigurjónsson, J., Stevick, P.T. and Øien, N. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Mar. Mammal Sci.* 15(1):1-32.
- Stevenson, M.R., Guillen, O. and de Ycaza, J.S. 1970. *Atlas de las Aquas Costaneras del Oceano Pacifico en la America del Sur*. Instituto Nacional de Pesca, Guayaquil, Ecuador. 80pp. [In Spanish].
- Stone, G.S., Flórez-Gonzalez, L. and Katona, S. 1990. Whale migration record. *Nature, Lond.* 346:705-6.
- Sutherland, W.J. (ed.). 1996. *Ecological Census Techniques*. Cambridge University Press, Cambridge. 352pp.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* 8:105-16.
- Tyack, P. and Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. *Behaviour* 83:132-54.
- Whitehead, H. 1985. Humpback whale songs from the North Indian Ocean. *Invest. Cetacea* 17:157-62.
- Whitehead, H. and Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* 60:2203-11.
- Winn, H.E. and Reichley, N.E. 1985. Humpback whale - *Megaptera novaeangliae* (Borowski, 1781). pp. 241-73. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 3. *The Sirenians and Baleen Whales*. Academic Press, London and Orlando. xviii+362pp.