Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground

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Abstract

Habitat preference is driven by a complex interaction among behavioural patterns, biological requirements, and environmental conditions. These variables are difficult to determine for any species but are further complicated for migratory marine mammals, such as humpback whales *Megaptera novaeangliae*. Patterns of habitat use in relation to social organization potentially exist for this species on their wintering grounds. Using an integrated GIS approach, we examined the degree to which spatial patterns of habitat stratification are correlated within different humpback whale group types from 6 years of sighting data (1996–2001) collected on the Antongil Bay, Madagascar, wintering ground. Stratification of humpback whale sightings by behavioural classification showed significant variation in depth and distance from shore. Distribution by depth could not be described as a function of group size but could be described as a function of social organization, with mother–calf pairs showing a strong preference for shallower water compared to all other group types. Group size and social organization seem to be factors in distribution by distance from shore. Significant diurnal patterns in distribution by depth and distance from shore also exist, where mother–calf groups maintain a relatively stable distribution and pairs and competitive groups are the most variable. Patterns of habitat preference on this wintering ground appear to be guided by social organization, where distribution by depth and distance from shore highlight areas critical to conservation.

Key words: habitat preference, social organization, geographical information system, humpback whale, *Megaptera novaeangliae*

INTRODUCTION

Social organization and patterns of habitat use are critical to understanding the distribution and behaviour of species in the wild. Organisms occupy regions that contain resources that meet their daily requirements (Burt, 1943), and spatial partitioning and social organization are often affected by the distribution and defensibility of these resources (Crook & Gartlan, 1966; Crook, 1970). Criteria for habitat selection, however, can be quite different for each organism. Distribution and differential patterns of habitat use may be based on seasonal fluctuations in availability of resources such as water (e.g. zebra and wildebeest, Kgathi & Kalikawe, 1993), availability of shelter and nesting sites (e.g. goby, Kroon, de Graaf & Liley, 2000), foraging strategies (e.g. lions, Funston *et al*., 1998) or a complex interaction of multiple factors (e.g. euglossine bees, Ackerman, 1983*a,b*). For some species, habitat selection and temporal distribution are driven more by access to conspecifics than by levels of predation or the availability of resources, such as food. Interspecific and intraspecific behaviour during these times is highly dependent on the mating system of the species (Emlen & Oring, 1977). Social behaviour has important implications for processes such as spatial distribution, reproductive success, and gene flow (Whitehead, 1997), and can therefore be an important variable when analysing habitat selection and use (Reed & Dobson, 1993; Dobson & Poole, 1998).

Questions concerning migration patterns and the habitat that large whales seek at the termini of their migrations have long been discussed (Townsend, 1935; Chittleborough, 1965; Dawbin, 1966). One such species, the humpback whale *Megaptera novaeangliae*, found throughout the three major oceanic basins (Indian, Atlantic and Pacific), undertakes an extraordinary migration from the nutrient-rich, high-latitude feeding grounds to lower-latitude tropical waters. During the winter months when mating and calving take place, humpback whales are regularly observed in tropical, near-shore waters and over shoals, banks, and offshore reef systems where they congregate with relatively high densities in disjunct localized regions (Dawbin, 1966; Balcomb & Nichols, 1982; Whitehead & Moore, 1982).

While in these lower-latitude regions, feeding behaviours are temporarily abandoned as post-partum females nurse their young and males compete for access to oestrous females (Tyack & Whitehead, 1983; Baker & Herman, 1984).

Specific habitat features sought by humpback whales in tropical waters remain largely unknown. Through long-term studies of the North Atlantic and North Pacific populations, it is generally accepted that humpback whales seek out warm, shallow, and somewhat protected water on their wintering grounds (Simmons & Marsh, 1986; Matilla *et al*., 1989; Katona & Beard, 1990). Several recent studies have examined some differential characteristics of this species on Hawaiian breeding grounds (Smultea, 1994; Craig & Herman, 2000). However, no long-term studies have classified or described habitat use and distribution of this species on a wintering ground.

Antongil Bay, located on the north-eastern coast of Madagascar, is a significant wintering ground for humpback whales in the south-western Indian Ocean (Rosenbaum *et al*., 1997; Rosenbaum, in press). The bay has a north-west–south-east orientation and extends 80 km inland with a mean width of 30 km. The extensive areas of shallow water that are characteristic of this bay match those which have been broadly described as the preferred environment for calving females of this species (Whitehead & Moore, 1982; Smultea, 1994; Rosenbaum *et al*., 1997). Since 1996, a suite of survey techniques (e.g. boat-based, shore-based and aerial) has been used to understand better the population structure and local habitat use of humpback whales wintering in Antongil Bay. Using an integrated GIS approach, the level and spatial patterns of habitat stratification within Antongil Bay were evaluated and correlations within different group types found on this wintering ground were examined. Our results provide detailed information on habitat preferences of humpback whales on a wintering ground and highlight areas that are critical to conservation initiatives.

METHODS

Study area

From the northernmost extent at Maroantsetra (49°44.3554′E, 15°26.1264′S) south to a line extending between Cap Antsirikira (50°09.6608′E, 15°59.6991′S) on the southernmost tip of the Masoala Peninsula and Bellone (49°51.2378′E, 16°13.5898′S) in the south-west, Antongil Bay covers an area of *c*. 2800 km² with 270 km of coastline extending 80 km inland. The bay has a mean depth of 41.5 m (SD = 19.4, max 70 m) with 44% of its waters being < 40 m in depth. With a mean width of 30 km, half of the bay is within 7 km from shore and is free of islands, with the exception of the extreme north where a chain of 5 small islands (total area 5.89 km²) exists, spanning a longitudinal expanse of 11.74 km. Surveys were launched from the northernmost island, Nosy Mangabe, and 97% of all sightings occurred in a
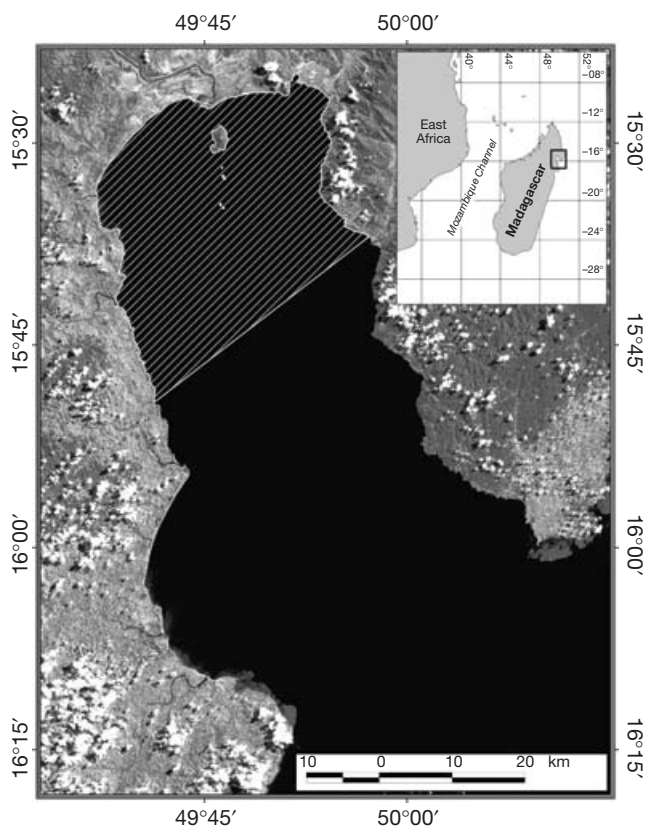

Fig. 1. Antongil Bay is *c*. 2800 km² with 270 km of coastline and a mean depth of 41.5 m (SD = 19.4 m). The focal study area, at the northern extent of the bay, encompasses 921 km² with a mean depth of 23 m (SD = 10.4 m).

921 km² region in the northern portion of the bay, referred to herein as the focal study area (Fig. 1). The mean depth within the focal study area is 23 m (SD = 10.4, max 46 m) with 84.5% of the area being evenly distributed between the depths of 10 m to 40 m; depths < 10 m and > 40 m are slightly under-represented (12.5% and 3%, respectively). Because of the small chain of islands bisecting the northern portion of the focal study area, half of the focal study area is within 4 km from shore.

Surveys

Daily observations in Antongil Bay were made from two 6-m fibreglass vessels between July and mid-September 1996–2001. The focal study area was partitioned into east and west regions of equal size. Each partition was further subdivided into 2.75 km² cells that formed the foundation for random transects. Transects were randomly generated by computer program and uploaded daily to global positioning system (GPS) receivers for each survey vessel. Randomized surveys were used to minimize sampling bias and ensure that trends associated with spatial and temporal distribution were detected. A Trimble GeoExplorer II GPS receiver with a customized data dictionary was used on each

survey vessel for navigation to and along transects, and for collection of positional data.

Data collection

A closing mode methodology was used in which the vessel left the previously determined transect to close on the group of whales sighted. Closing mode methodologies allow for individual identification, genetic sampling, and more accurate determination of behaviour and group size (Barlow, 1997). The vessel returned to the transect when possible once the group had been completely sampled or the maximum time limit was reached. Maximum time limits were imposed so as not to stress the individuals in the group or affect their behaviour. Upon completion of daily surveys, positional data were downloaded from the GPS receivers and exported for archive and import into a database for analysis.

When whales were encountered, the initial and termination positions of the group were recorded in addition to descriptive attributes. Groups of whales were classified into 1 of 5 classes (mother–calf pairs, M/C; mother–calf–escort, M/C/E; pairs; competitive groups; singletons), based on observed attributes or behavioural characteristics previously described for this species (Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham *et al.*, 1992). All group sightings recorded as singers involved a solitary animal and were considered singletons for this analysis. Group sightings used in this analysis represent 86.5% of all groups observed in Antongil Bay; 10.5% of all group sightings did not have sufficient associated positional information. Groups that were characterized in the field by extremely short association times (3% of all sightings) were excluded from the analysis because of the fluid nature of these associations, for which accurately documenting group type, behaviour and social organization was difficult.

Spatial analysis

Soundings from nautical charts and a series of 1:100 000 topographic maps, which also display depth characteristics for Antongil Bay, were manually digitized using ESRI's software PC ARC/INFO and ArcView (version 4.0 and 3.2a, respectively). Soundings were then co-registered to a series of user-collected ground control points and orthorectified Landsat data using PCI Geomatica (version 8.0). A finer scale coastal boundary was derived from the orthorectified Landsat data and combined with the digitized soundings to create a 3-dimensional surface model of Antongil Bay with a 100×100 m cell size. Depth values between known locations (soundings and coastal and island boundaries) were interpolated (Burrough & McDonnell, 1998; Sear & Milne, 2000) using a combination of algorithms and modules provided in the Spatial Analyst and 3D Analyst extensions for ArcView, as well as additional customized programs developed by PJE. A secondary raster dataset was created at the same resolution and spatial extent as the surface model, but with distance to the nearest coastal feature (distance from shore) as cell values rather than depth.

Importing the positional records for each group sighting created a data layer that was superimposed over the 3-dimensional surface model. By superimposing the data layers, the depth for each group sighting was inferred from the underlying surface model and joined as an additional attribute to each positional record. In addition to depth, distance from shore was calculated for each group sighting and joined as an attribute for each positional record.

Analysis

Quantitative profiles were derived separately for the whole bay, focal study area and individual group sightings. The raw depth and distance from shore datasets for the entire study site were merged using a computationally simple and reversible algebraic combinatory technique (Ersts, 2001) and exported, in dBASE format, for analysis in an external statistics package (SPSS version 10.1). Likewise, depths and distance from shore values, which were spatially joined with each positional record, were exported for analysis in an external statistics package. Raw depths in each dataset were binned into 5 and 10 m intervals while distance from shore values were binned into 500 and 1000 m intervals. Binned values were used to report the bathymetric characteristics of the bay and percentages of group types encountered by depth and distance from shore. Raw data values were used to compute all other statistics.

Because of the conservation implications, a fine scale analysis was deliberately used to test depth and distance from shore independently. Tests for homogeneity of variance, using the Levene test, on the raw (non-binned) depth and distance from shore values indicated that there were significant differences in variances; thus non-parametric methods were used in this analysis. One-factor analyses were conducted using a Kruskal–Wallis test and subsequent pair-wise comparisons were accomplished using the Mann–Whitney U-test to evaluate heterogeneity among different classes of animals for water depth and distance from shore. For general dispersion indices, geographical arithmetic means (centroids) for each thematic category (year and group type) were computed from the positional data and distances to the centroid for the respective category were calculated and joined as an attribute to each positional record.

RESULTS

Correlation of depth and distance from shore

For Antongil Bay, linear regression of 1 km distance bins and mean depth within each bin exhibited a strong relationship ($r^2 = 0.870$, $n = 20$, $P < 0.001$). Similar results existed for the focal study area ($r^2 = 0.916$, $n = 20$, $P < 0.001$). The coefficient of variation for depth measurements in each 1 km distance bin decreased

logarithmically for both the whole bay and the focal study area ($r^2 = 0.985$, $n = 20$, $P < 0.001$ and $r^2 = 0.945$, $n = 16$, $P < 0.001$, respectively). Coefficient of variation ranged from 92.9% at 1 km to 3.4% at 20 km for the whole bay and 73.3% at 1 km to 1.2% at 16 km for the focal study area. These results indicate that there is considerable variation in depth, especially in the near-shore regions. These results were not unexpected since Antongil Bay is bordered on three sides by mountains and resembles an inverted 'U' in shape, with the deepest waters being found between main coastal features, rapidly becoming shallow toward shore.

Temporal variation of depth and distance from shore

Between 1996 and 2001, during 1876 h of boat-based surveys, 63% of all groups were observed within 5 km from shore and 80% of all groups were observed at depths no greater than 30 m. Depth and distance from shore showed significant variation among group types (Kruskal–Wallis ANOVA $\chi_4^2 = 12.22$, $P = 0.016$ and $\chi_4^2 = 13.75$, $P < 0.01$ respectively). After examining temporal aspects, no significant difference in depth was detected among years for all groups (Kruskal–Wallis ANOVA $\chi_5^2 = 2.86$, $P > 0.70$), but a significant difference was found to exist among months (Kruskal–Wallis ANOVA $\chi_2^2 = 6.57$, $P = 0.037$) with groups being encountered in deeper water as the season progressed from July to September.

Distance from shore showed a highly significant difference among years (Kruskal–Wallis ANOVA $\chi_5^2 = 28.64$, $P < 0.0001$), but no significant difference among months (Kruskal–Wallis ANOVA $\chi_2^2 = 0.97$, $P > 0.60$). However, there was no significant difference by year in the distance from the individual sightings to the geographic mean (centroid) of sightings for each year (Kruskal–Wallis ANOVA $\chi_5^2 = 7.03$, $P > 0.20$), which indicated that the geographic extents for each year were roughly equivalent. In examining the mean geographical position for each year, the centroid for 1997 was found to be located 4.6 km south of the mean centroid location for the remaining years, which are themselves positioned at a mean distance of 1.05 km (SD = 0.57 km) around the mean centroid location (Fig. 2). Upon removing the 1997 data from the analysis, distance from shore did not show any significant difference among year or month (Kruskal–Wallis ANOVA $\chi_4^2 = 4.23$, $P > 0.30$ and $\chi_2^2 = 3.10$, $P > 0.20$, respectively). This result was not unexpected because there was an exploratory effort to expand the survey effort as far south as possible during the second year of the study (1997). Inclusion or exclusion of the 1997 data did not significantly influence results for any test other than the among year comparison.

Depth and distance from shore associations for group types

Of all groups observed in Antongil Bay, 66% were either pairs of whales or male-dominated groups consisting of
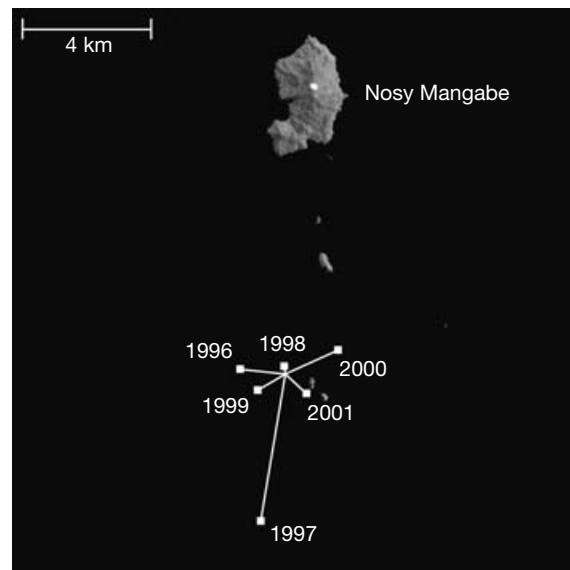

Fig. 2. Sighting centroids for humpback whales *Megaptera novaeangliae* by year.

Table 1. Mann–Whitney *U*-test showing differential use of depth among humpback whale *Megaptera novaeangliae* group types for 1996 to 2001 sightings (cells contain *P*-values)

	M/C/E	Pair	Competitive	Singleton
M/C	0.060	< 0.01	< 0.001	< 0.003
M/C/E		0.883	0.627	0.645
Pair			0.192	0.328
Competitive				0.923

three or more whales exhibiting competitive behaviour. Females with young (M/C and M/C/E) accounted for 12% of all sightings. Mother–calf pairs showed a preference for shallow water. Of all mother–calf pairs, 60% were observed in waters < 20 m deep, while similar proportions of mother–calf–escorts (59.5%), pairs (61%), competitive groups (61.5%) and singletons (67%) were observed in waters ≥ 20 m deep (Fig. 3). Mann–Whitney *U*-tests (Table 1) indicated that mother–calf pairs showed marginally significant differences from mother–calf–escorts in their depth preference but were significantly different from all other group types. Furthermore, depth did not vary significantly with respect to the number of individuals per group (Kruskal–Wallis ANOVA $\chi_{10}^2 = 13.20$, $P > 0.2$).

Of all females with calves, 95% were observed within 7 km from shore. Additionally, 20% of all mother–calf pairs, the single highest percentage of any group type in all other distance bins, were observed within 1 km of shore and no escorted mother–calf pairs were observed beyond 7 km from shore (Fig. 4). Competitive groups were observed at a mean distance of 4.6 km (SD = 2.9 km) from shore while all other groups were observed at a mean distance of 3.9 km (SD = 2.8 km). Mann–Whitney *U*-tests (Table 2) indicated that competitive groups were significantly different from mother–calf pairs, mother–calf–escorts and pairs, with respect to distance from
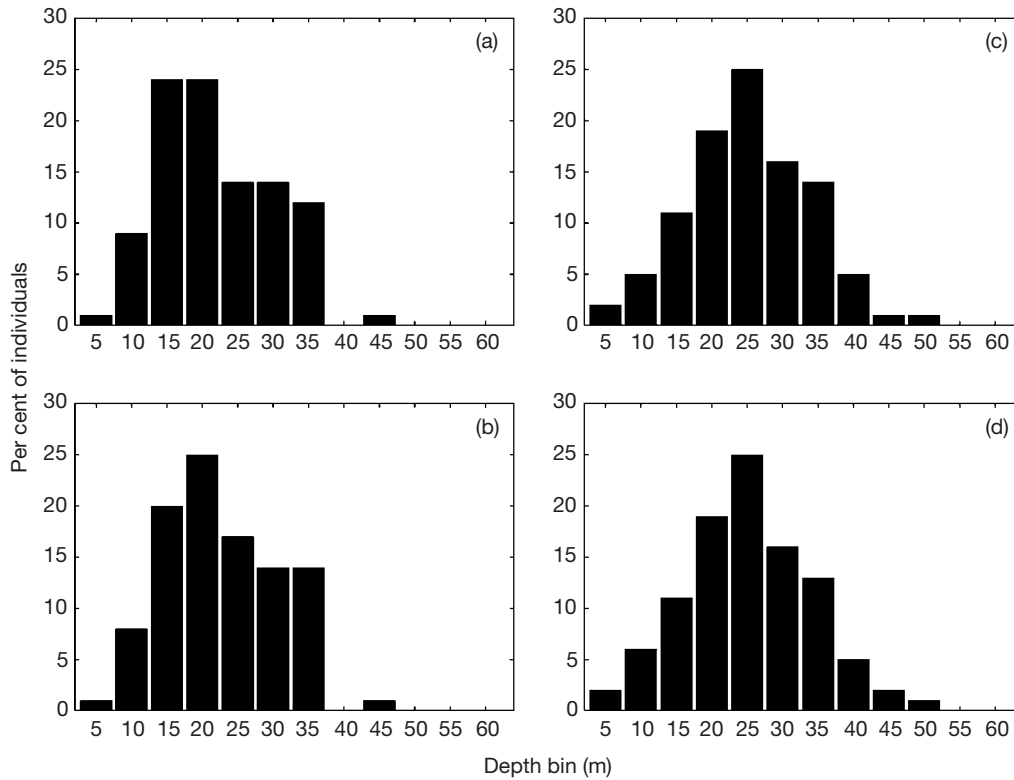
Fig. 3. Distribution of whales *Megaptera novaeangliae* by depth bin and group type: (a) mother–calf pairs (b) mother–calf pairs and mother–calf–escorts (c) mother–calf–escort, pairs, competitive groups, and singletons (d) pairs, competitive groups and singletons.
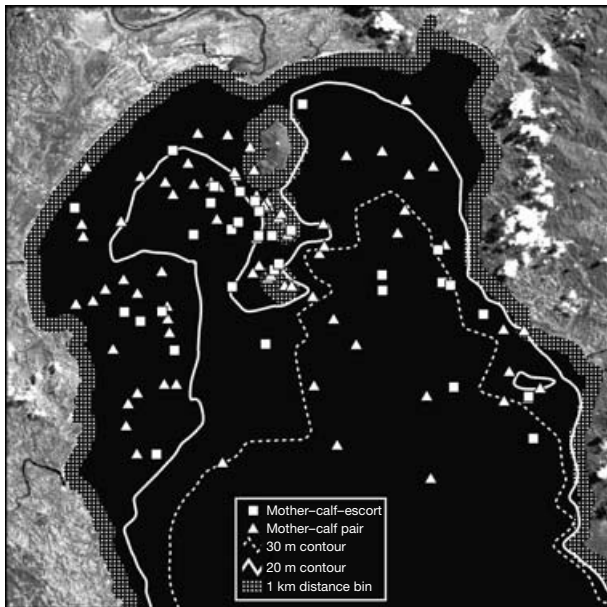

Fig. 4. Distribution of escorted and non-escorted mother–calf pairs of humpback whales *Megaptera novaeangliae* in relation to depth and distance from shore.

Table 2. Mann–Whitney *U*-test showing differential use in distance from shore among humpback whale *Megaptera novaeangliae* group types for 1996 to 2001 sightings (cells contain *P*-values)

	M/C/E	Pair	Competitive	Singleton
M/C	1.0	0.120	< 0.001	0.090
M/C/E		0.248	0.015	0.163
Pair			0.021	0.761
Competitive				0.137

measurable variation occurred with distance from shore for groups with three or fewer individuals (Kruskal–Wallis ANOVA $\chi_2^2 = 1.24$, $P > 0.5$), but groups with four or more whales showed marginal variation (Kruskal–Wallis ANOVA $\chi_2^2 = 13.34$, $P = 0.064$). Linear regression of competitive group size and mean distance from shore showed a positive relationship ($r^2 = 0.854$, $n = 9$, $P < 0.001$), indicating that larger competitive groups were more frequently observed farther from shore.

Diurnal changes in depth and distance from shore

Group sightings with increasing depth and distance from shore categories were observed from sunrise to midday and decreased again as sunset approached (Fig. 5). Whales in Antongil Bay showed a highly significant variation
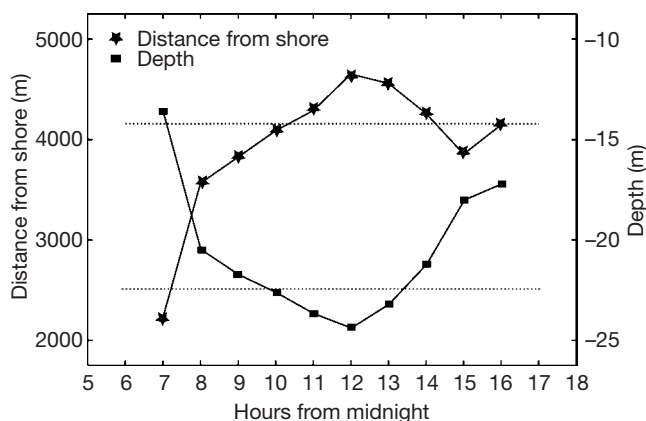
shore. When group classification was removed, there was significant variation in distance from shore with respect to group size (Kruskal–Wallis ANOVA $\chi_{10}^2 = 21.36$, $P = 0.019$). A finer analysis by group size indicated that no

Fig. 5. Diurnal variation in use of depth and distance from shore by humpback whales *Megaptera novaeangliae*. Dashed line, mean values for each variable.

(Kruskal–Wallis ANOVA $\chi^2_{11} = 42.51, P < 0.0001$) in distribution by depth through the day and a moderate variation (Kruskal–Wallis ANOVA $\chi^2_{11} = 21.18, P = 0.032$) with distance from shore.

Partitioning these data by group type and time of day revealed marginal variation in depth for pairs (Kruskal–Wallis ANOVA $\chi^2_9 = 16.32, P < 0.06$) and significant variation for competitive groups (Kruskal–Wallis ANOVA $\chi^2_{10} = 25.45, P < 0.005$). Furthermore, competitive groups with three to five whales did not exhibit variation throughout the day with depth and distance from shore (Kruskal–Wallis ANOVA $\chi^2_{10} = 11.10, P > 0.3$ and $\chi^2_{10} = 3.98, P > 0.9$ respectively), while competitive groups with more than five whales did exhibit significant variations in these two variables (Kruskal–Wallis ANOVA: depth, $\chi^2_8 = 18.54, P = 0.018$; distance from shore, $\chi^2_8 = 16.14, P = 0.04$).

DISCUSSION

There can be considerable differences in resources used by feeding and breeding aggregations in highly mobile organisms or organisms that undertake long migrations. For humpback whales, Caughley & Gunn (1996) provide the most appropriate definition of habitat, where habitat is broadly discussed as a suite of resources and biotic and abiotic environmental variables that determine the presence, survival and reproduction of a population. Habitat preference is subsequently driven by a complex interaction among behavioural patterns, biological requirements and environmental conditions. Habitat use and preference are difficult variables to determine for any species and the identification of key variables that describe the distribution of humpback whales on their wintering grounds is further complicated by their inconspicuous, highly mobile nature and characteristically dynamic social affiliations. Our work is the first long-term, fine-scale study that highlights the importance of social organization, depth and distance

from shore as initial variables for determining habitat stratification in humpback whales on a wintering ground.

Previous studies on this species provide only anecdotal information of habitat use on their wintering ground or simply note the presence or absence of humpback whales around islands, in bays or on shallow banks. Sea surface temperature, hydrographic features and other variables derived from satellite data have recently been used as predictors of cetacean habitat and distribution (Smith *et al*., 1986; Jaquet, Whitehead & Lewis, 1996; Moses & Finn, 1997; Hooker, Whitehead & Gowans, 1999; Davis *et al*., 2002). Hooker *et al*. (1999) described cetacean distribution using four variables (depth, slope, sea surface temperature and month) and found that depth was the most informative variable. Gregr & Trites (2001) examined historical distributions using the same four variables plus salinity and a categorical depth class. Based on results of their analysis, these authors concluded that the predictive power of these variables is rather weak, suggesting that humpback whale habitat is better described by other factors. Each of these studies, however, attempted to describe the distribution of whales on their feeding grounds rather than on their breeding or wintering grounds. In our analysis, depth and distance from shore were chosen as our major variables because these variables are more relevant to a wintering area and additional fine-scale water column datasets (e.g. salinity and turbidity) and physical characteristics (e.g. bay floor composition) are not available for this region.

Humpback whales aggregate in Antongil Bay primarily for the purpose of mating, giving birth and nursing and do not display behaviours (e.g. feeding and territorial or resource guarding) that are frequently used to delineate habitat use and preference. Consequently, social structure associated with mating strategies becomes a critically important variable. Using an integrated GIS approach, our data show that habitat use and preference on the Antongil Bay wintering ground are best determined by social organization in a spatial context.

Randomized surveys were used to minimize sampling bias; however, because of the nature of the methodology used for the individual identification of whales, more effort tends to be applied to areas with higher concentrations of whales. As a result, there is probably some degree of spatially non-uniform application of effort. In addition, our positional data only represent the locations of the initial contact with a group, thus not accounting for variations in depth during the period of observation. Travelling or meandering were not behaviours systematically recorded for every group, so all points were used in the analysis regardless of whether they seemed to be outliers. While these effects could introduce some bias into the degree to which stratification is apparent, they do not compromise the overarching results.

Stratification of humpback whale sightings by group classification shows significant variation in depth and distance from shore. These findings are stable across years; however, monthly variation in depth was found to exist. Behaviour exhibited by humpback whales is determined by the category of individuals present on

the wintering ground throughout the season (Herman & Antinoja, 1977; Baker & Herman, 1984; Simmons & Marsh, 1986). Consequently, differential migration by age, reproductive category (e.g. pregnant females and females near the end of lactation) and gender (Chittleborough, 1965; Dawbin, 1966; Best, Sekiguchi & Findlay, 1995) is a probable explanation for the observed temporal variation in distribution by depth. Distribution by depth could not be described as a function of group size but could be described as a function of social organization, with mother–calf pairs showing a strong preference for shallower water (< 20 m deep) compared to all other group types.

Group size and social organization seem to be factors influencing distribution by distance from shore; however, this variable is better described in the context of social organization. Competitive groups were consistently found farther away from shore compared to mother–calf pairs, mother–calf–escorts and pairs. Unpublished observations (Bauer, 1986 cited in Smultea, 1994) state that larger groups are found farther from shore and our data indicate that a strong relationship does exist between distance from shore and the number of individuals participating in a competitive group; larger competitive groups are found farther from shore.

Gender determination, using genetic techniques, has revealed that a significant number of pairs and smaller competitive groups (three individuals) observed in Antongil Bay were actually male dyads or all-male groups (C. Pomilla & H. C. Rosenbaum, pers. obs.). These male dyads and smaller all-male groups may frequent the shallower near-shore regions in search of receptive females. During this time, group cohesion may be very fluid. Once a female became the focal member of the group, male interactions quickly changed from searching behaviours to more intense male–male competition and defence. This change in behaviour may also represent a need for a change in habitat, whereby deeper waters, farther from shore, could be sought to allow greater movement within the water column. Alternatively, competitive groups in deeper water may represent non-regular movements of the group resulting from dynamics of male–male competition.

The percentage of mother–calf pairs found within 1 km from shore represents the single highest percentage of any group type in all other distance bins. This result, and the fact that no escorted mother–calf pairs were found beyond 7 km from shore, indicates that near-shore regions are especially important for females with calves. It is probable that mother–calf pairs seek out these near-shore regions for protection against rough sea conditions (Whitehead & Moore, 1982; Mattila & Clapham, 1989), conspecifics (Smultea, 1994) or large predators (Dolphin, 1987; Flórez-González, Capella & Rosenbaum, 1994; Smultea, 1994; Corkeron & Connor, 1999). Escorted and non-escorted mother–calf pairs showed marginally significant differences in depth preference, with escorted mother–calf pairs typically being found in deeper water. This result supports previous assertions that females not wanting to be courted move toward sheltered water to discourage pursuing males (Mattila *et al*., 1989); or for multiple escorts, to influence the selection of the primary escort (Glockner-Ferrari & Ferrari, 1985) by limiting the amount of movement during challenges and thus the possibility of displacement. Additionally, it is highly probable that females with young acquire an escort while they are in transit between key areas or on short exploratory ventures or 'training runs' for their calves into deeper, less protected waters.

Humpback whales in Antongil Bay also showed significant diurnal patterns in distribution by depth and distance from shore. These diurnal patterns seem to be driven by group-specific behaviours and are best described in terms of the social structure rather than number of individuals participating in the group. This is most obvious in groups with two (mother–calf pairs and pairs) or three (mother–calf–escort and competitive groups) individuals where differences in habitat use were considerable. Group encounters during the early morning and late afternoon were more likely to occur closer to shore in shallower water while group encounters around midday were typically in the deepest water and farthest from shore. Comparison by group type indicates that mother–calf pairs, mother–calf–escorts and singletons maintained a relatively stable distribution by depth and distance from shore while pairs and competitive groups were the most variable. Whales in Antongil Bay used the shallower waters closer to shore for resting, particularly during the early morning and late afternoon, and moved toward deeper waters farther from shore during the day while engaging in competitive behaviour or in transit.

Variation observed throughout the day was similar to Helweg & Herman's (1994) accounts of diurnal behavioural patterns of humpback whales in Hawaiian waters, which were characterized by low levels of activity in the early morning with a peak in energetic aerial behaviours and male–male competition at midday and mid-afternoon. Direct comparison, however, between the two datasets is difficult because of the inherent differences between shore-based and boat-based survey methodologies.

Identification of habitat use and social organization are important aspects for evaluating distribution and behavioural patterns of species. Understanding these patterns of habitat use and social organization highlight areas where critical human–animal conflicts may occur. For humpback whales on their breeding grounds, these interactions can occur in areas of overlapping use by humans and certain classes of whales, where increased disturbance may have significant implications on short-term residency patterns and individual survivorship. Preference shown by females with calves for shallower waters and, more importantly, the preference shown for near-shore regions occurs in areas that are also heavily used by humans for coastal trade, commercial and subsistence fishing, whale-watching and recreation. Findings such as these are important for furthering our understanding of habitat preference and use, but are also central to the development of protected areas, conservation initiatives and management plans.

Acknowledgements

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