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Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipelago breeding region, Bahia, Brazil

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To characterize temporal patterns of humpback group structure around Abrolhos Archipelago, Brazil, seven years (1998–2004) of data obtained from July through November were analysed. During one-hour scans, observers determined group composition within 9.3 km around a land-based station. A total of 930 scans, comprising 4288 groups were analysed. Seven group categories were identified and their frequencies were 14.6% of 1AD (lone whale), 25.2% of DYAD (two adult whales), 7.3% of TRIO (three adult whales), 5.2 of TRIO+ (more than three adults), 24.9% of MOC (mother and calf), 19.6% of MOCE (mother, calf and one escort), and 3.1% of MOCE+ (mother, calf and more than one escort). Proportions of whale-group categories did not change between morning and afternoon, nor among years. However, as the season progressed, groups with calves increased while groups without calves decreased. This progression may be explained by the segregated migration patterns of humpback whales and also by changes in the social status of individuals. The Abrolhos Reef provides protection from the prevailing winds, which may explain the higher proportion of groups with calves in the area.

INTRODUCTION

The humpback whale is a cosmopolitan species that undertakes extensive, seasonal migrations between high-latitude feeding grounds in summer and low-latitude winter breeding grounds (e.g. Dawbin, 1966). Migratory timing varies with age, sex and reproductive status (e.g. Craig et al., 2003). Lactating females with their calf from the previous year (yearling) arrive first in breeding areas, followed by immature individuals, mature males, 'resting' females (those neither pregnant nor lactating) and lastly pregnant females (e.g. Dawbin, 1966). As the winter breeding season progresses, the whales leave the breeding ground in reverse order: females with calves are the last to leave for summer feeding grounds (Dawbin, 1966).

Breeding and calving grounds of the humpback whale are typically found near islands or offshore reef systems in tropical or subtropical waters (e.g. Dawbin, 1966). For many years, Abrolhos Bank was considered the only known breeding and calving ground for humpback whales in the western South Atlantic (Martins et al., 2001), however, the humpback population that winters off the Brazilian coast has increased in numbers (Freitas et al., 2004) and humpback whales are being encountered along the coast (Pizzorno et al., 1998; Zerbini et al., 2004). The area surrounding Abrolhos Archipelago is considered unique because of the high concentration of whale groups with calves (Martins et al., 2001; Morete et al., 2003).

Social behaviour of humpbacks in their breeding grounds has been studied mainly in Hawaii and in the Caribbean (e.g. Herman & Antinoja, 1977; Mobley & Herman, 1985; Mattila et al., 1994). Observations of humpback whale social behaviour in Brazil are rare and generally have not been the primary focus of studies as in Martins et al. (2001).

Humpback whale social behaviour is characterized by small groups and brief associations, with occurrences of lone individuals, dyads and trios being common (e.g. Mobley & Herman, 1985). Martins et al. (2001) noted that lone, dyad and mother–calf pairs were the most frequent whale-group categories observed at Abrolhos Bank.

The research findings reported here represent seven years of data collected from a land-based observation station focused on the general and temporal patterns of humpback whale social structure around Abrolhos Archipelago.

MATERIALS AND METHODS

Study area

Abrolhos Bank (16°40' to 19°30'S and 37°25' to 39°45'W) is located on an extension of the Brazilian continental shelf on the east coast of Brazil (Figure 1). The Bank is a mosaic of coral reefs, mud and calcareous alga bottoms with warm (winter average temperature=24°C) and shallow (average depth: 15–20 m) waters (Ibama/Funatura, 1991).

The land-based observation station (17°57'44"S 38°42'22"W) was established 36 m above sea level on the western portion of Santa Barbara Island in the Abrolhos Archipelago. From the station the observers surveyed a radius of 9.3 km (5 nautical miles) surrounding the station, except for two areas hidden by islands. These two blind spots, one to the east and one to the west, obscured arcs of 8° and 14° respectively. Excluding these blind spots, the study area

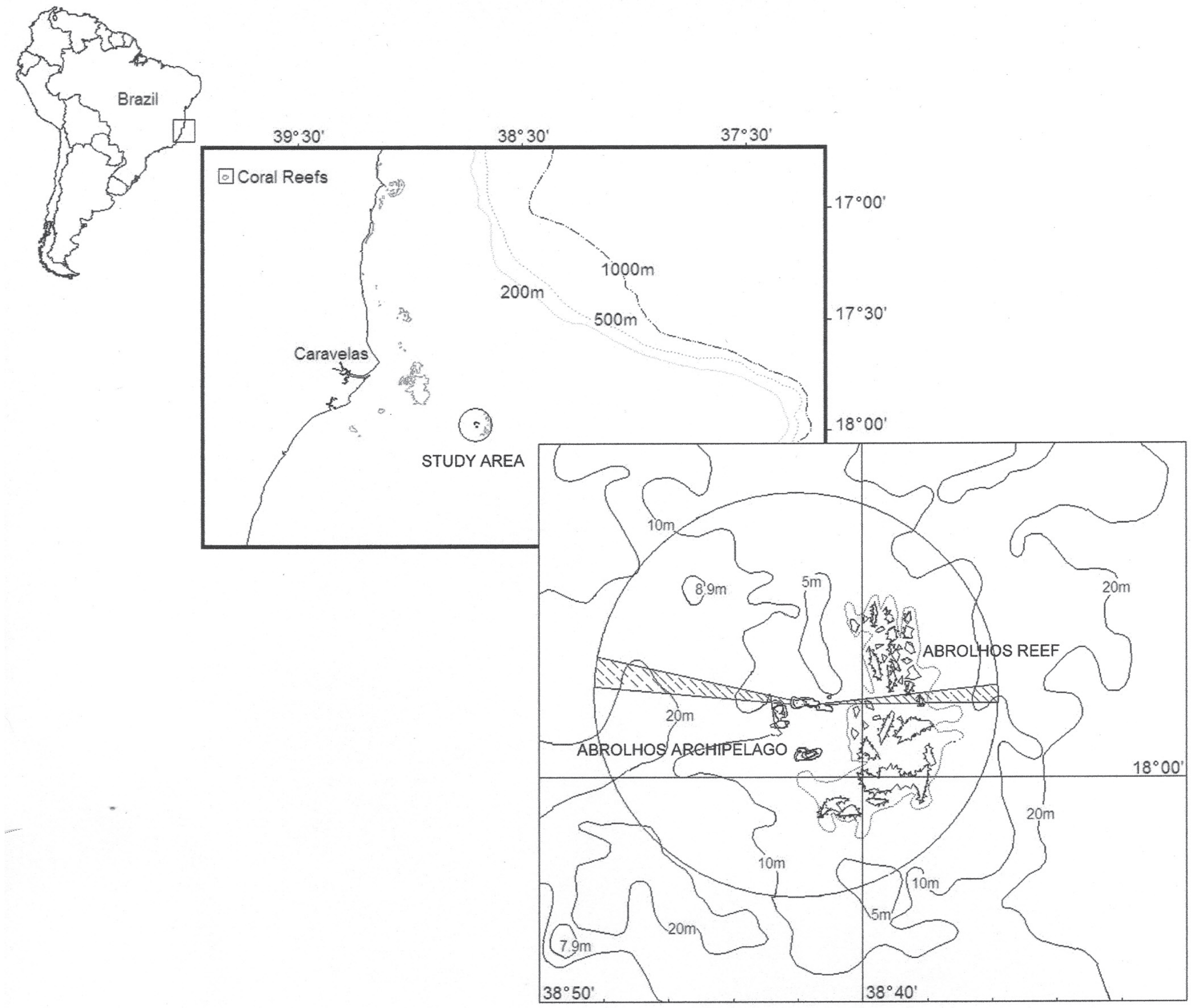

Figure 1. Location of the Abrolhos Archipelago on the east coast of Brazil and the study area, which encompasses a 9.3 km radius (excluding the two blind areas to the east and west) from the land-based station on Santa Barbara Island.

was approximately 250 km^2 with a maximum water depth of 20 m. The Abrolhos Reef, which is a typical reef formation (14 km long by 6 km wide), covers approximately one quarter of the area from the north-east to the south-east (Figure 1).

Definitions

A season was defined as the period when humpback whales were in the Abrolhos region, from the months of July through November. A whale group was defined as either a lone whale or affiliations of whales with members of the group within 100 m of each other, generally moving in the same direction in a coordinated manner (e.g. Mobley & Herman, 1985). A calf was defined as an animal in close proximity to another whale, visually estimated to be less than 50% of the length of the accompanying animal (Chittleborough, 1965). All non-calf whales were considered to be adults because of the impossibility of visually distinguishing subadults from mature individuals. A whale in close proximity to a mother and calf pair was designated as an 'escort'. Studies conducted in other humpback whale breeding grounds using biomolecular methods to determine the sex of escorts and underwater observations of the genital region of these animals suggest that all escorts are male (e.g. Glockner-Ferrari & Ferrari, 1985; Medrano et al., 1994). In this study whale groups were divided into seven categories: one adult whale alone (1AD); two adult whales (DYAD); three adult whales (TRIO); more than three adults (TRIO+); mother and calf (MOC); mother and calf and one escort (MOCE); mother and calf and more than one escort (MOCE+).

Observations

Humpback whale groups were observed during one-hour scans almost daily during July through November of 1998–2004. Data were not collected during rainy days, when wind speed was greater than 20 knots, and when sighting conditions were considered poor by the observers due to haze, glare and cloud coverage. In order to characterize temporal patterns in the relative proportion among humpback whale group categories, scans were separated into morning and afternoon (seven years combined), three phases during the season (seven years combined) and years. Morning scans were conducted from 0545 to 1125 h (local time) and afternoon scans were conducted from 1225 to 1645 h. Observations within seasons were separated into three phases 'A', 'B' and 'C'. Because the number of humpback whales sighted and the date of peak numbers varied during and among seasons (M.E. Morete, unpublished data), to avoid any effect of whale numbers in behavioural pattern, these phases were

Table 1. *Beginning and end dates of phase 'A', 'B' and 'C' for each season. The number of scans for each phase is in parentheses. Phase 'B' has 50 days.*

Season (No. days)	Phase 'A' (No. scans)	Phase 'B' (No. scans)	Phase 'C' (No. scans)
1998 (148)	3 July–12 August (51)	13 August–1 October (57)	2 October–27 November (53)
1999 (148)	4 July–2 August (27)	3 August–21 September (46)	22 September–28 November (61)
2000 (147)	6 July–6 August (31)	7 August–25 September (54)	26 September–29 November (69)
2001 (144)	5 July–4 August (33)	5 August–23 September (49)	24 September–25 November (45)
2002 (144)	6 July–5 August (31)	6 August–24 September (30)	25 September–26 November (57)
2003 (140)	6 July–29 July (17)	30 July–16 September (41)	17 September–22 November (66)
2004 (127)	7 July–4 August (23)	5 August–22 September (45)	23 September–10 November (44)

calculated differently for each year. For each year the daily counts of whales were used to predict the highest whale count using a negative binomial generalized linear model (M.E. Morete, unpublished data), and this highest predicted count was associated with a specific date that represented the mid-point of each season. This date determined the mid-point of the 'B' phase, which always had 50 d, as the whole season would theoretically have 150 d. Phase 'A' comprised the days from the beginning of the season to the beginning of phase 'B', and phase 'C' comprised the days from the end of phase 'B' to the last day of the observation period. Because the observation periods started and ended on different dates in each year and due to meteorological reasons, the numbers of days and scans in phase 'A' and phase 'C' varied (Table 1). In this manner phase 'A' represents the beginning of the season, phase 'B' the middle of the season and phase 'C' the end of the season.

For this analysis, the number of whale sightings was analysed rather than sightings of individual whales. Within a single scan, the same individual whale was not recounted, so observations within the scan are independent. However, it was not possible to identify individual whales from the land-based observation station, so among scans it was possible that groups containing individuals previously observed during different periods, phases and seasons were re-observed, but we assumed that whale sightings were independent.

During each scan, three observers searched in all directions for humpback whale groups within a radius of 9.3 km of the land-based observing station. The search was unsystematic in that there was no pre-determined period of time to search for whales in each direction, and two observers would each search a 180° arc with the naked eye and 7×50 binoculars. Whales were usually spotted by their blows, a splash caused by active behaviour or exposure of a part of their body. Once a whale group was sighted, the principal observer observed that group with a theodolite (30-power monocular magnification) for at least three surfacings or until group size and composition were determined. While observing the whales, the observer using the theodolite noted unique characteristics of animals in the group (i.e. scars, natural markings, the shape of dorsal fin) to distinguish the group from any other group in close proximity so as to avoid double counting. Occasionally whale groups were observed longer than the one-hour sample period to accurately determine the group's composition. If movement of several whale groups was concentrated in one area and there was uncertainty if a group had already been registered, the scan was cancelled, data were discarded and a new one-hour scan was begun.

Statistical analyses

A contingency table was constructed to aggregate all whale group sightings in each time frame (i.e. morning and afternoon, phases and seasons). To eliminate differences in sighting effort among time frames and to eliminate bias due to the fluctuation in the number of groups of whales among time frames, the number of each whale-group category sighted in each phase was divided by the total number of groups sighted in that phase to provide the percentage of whale groups representing each group category. The Shapiro–Wilk test was used to test the normality of the data and the Levene test was used to test the homogeneity of variance. Because some data were not normally distributed and/or the variance was not homogeneous, data were rank transformed and an analysis of variance on these ranks was applied. For phases and seasons, the Tukey honestly significantly different (HSD) was used as a *post-hoc* test to verify differences among each phase and each season. All statistical computations were performed using the software SPSS v. 11 for Windows.

RESULTS

A total of 930 one-hour observation scans was made. These scans were separated into 509 morning scans and 421 afternoon scans and 213 scans in phase 'A' (837 humpback groups sighted), 322 scans in phase 'B' (2428 groups) and 395 scans in phase 'C' (1023 groups). No whales were observed during 101 scans (10.8%). Of the remaining 829 scans, 4782

Table 2. *Tukey HSD results for rankings of the proportions of humpback whale group categories in phases 'A', 'B' and 'C' for the seven winter breeding seasons. The Bonferroni correction was* α*=0.007.*

	Phases (P)		
Group	A–B	A–C	B–C
1AD	0.762	0.014	0.073
DYAD	<0.001	<0.001	<0.001
MOC	<0.001	<0.001	<0.001
MOCE	<0.001	<0.001	<0.001
MOCE+	0.001	<0.001	0.289
TRIO	0.076	<0.001	0.001
TRIO+	0.328	0.001	0.029

For definitions of abbreviations see text.

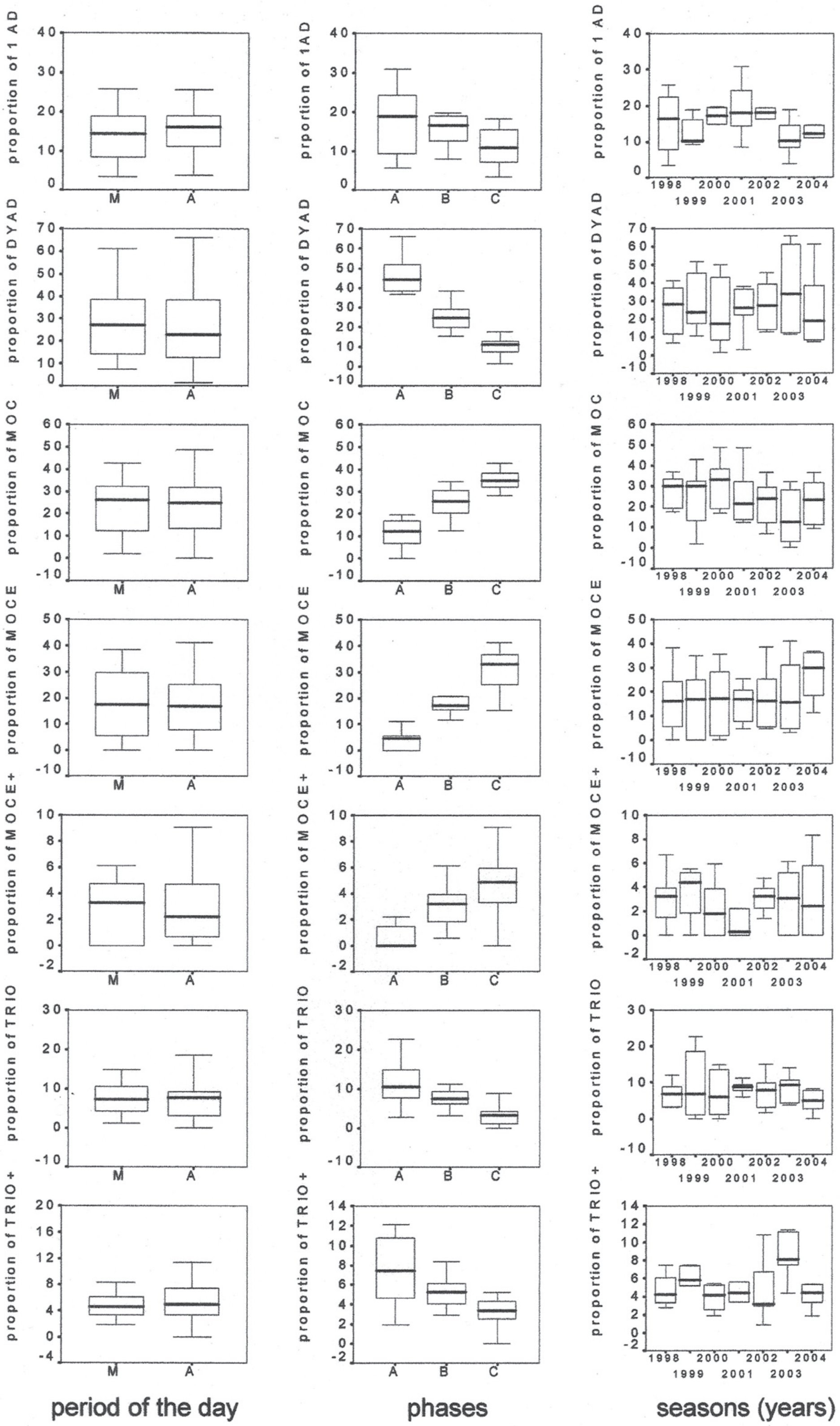

Figure 2. Mean proportion of whale-group categories during morning 'M' and afternoon 'A', in phases 'A', 'B' and 'C', and in seasons. Note the different scales on the Y-axis to better illustrate the temporal patterns. Box plots represent the median and quartile, where extreme values were excluded.

groups were observed. Among these, 494 (10.3%) groups were considered indeterminate and therefore were excluded from the analyses, while the remaining 4288 (89.7%) groups included 10,044 humpback whales (2044 calves and 7996 adults). Of the total number of accepted groups, 2244 (52.3%) were groups without calves, and 2044 (47.7%) with calves. The frequency of each humpback group category was 14.6% of 1AD, 25.2% of DYAD, 7.3% of TRIO, 5.2%

of TRIO+, 24.9% of MOC, 19.6% of MOCE and 3.1% of MOCE+. Among whale groups that included calves, 52.3% were MOC, 41.2% MOCE and 6.5% MOCE+. There was one sighting of a group with three adults and two calves and it was excluded from the analyses. The mean proportion of whale-group categories during morning and afternoon, in phases 'A', 'B' and 'C' and in the seasons are shown in Figure 2.

There was no statistical evidence that the distribution of the ranked proportion of each whale-group category varied between morning and afternoon or among years. However, there were statistically significant differences in the distribution of whale-group categories among the 'A', 'B' and 'C' phases of the season (Figure 2). The proportion of groups containing calves (i.e. MOC, MOCE, MOCE+) increased as the seasonal phases progressed, from the lowest proportion (17.3%) in phase 'A' to the highest proportion (72.3%) in phase 'C'. In contrast, the proportions of whale groups without calves (i.e. DYAD, TRIO and TRIO+) decreased from phase 'A' to 'C'. However, there was no statistical evidence that the proportion of groups of 1AD varied among phases. For all other group categories, the Tukey HSD test suggested strong evidence that phases 'A' and 'C' were different when all years were combined. Phases 'A' and 'B' were also different except for groups of TRIO and TRIO+. Between phases 'B' and 'C', with exception of TRIO+ and MOCE+, group categories varied (Table 2).

Among phases, when only whale groups with calves were analysed, the distribution of data relative to the proportion of MOC, MOCE, and MOCE+ did not change ($0.23<P<0.42$).

DISCUSSION

This study corroborates previous studies, which reported high frequencies of whale groups with calves around Abrolhos (Martins et al., 2001; Morete et al., 2003). The proportion of groups with calves encountered in this study area was much larger than other important humpback whale breeding areas such as Maui, Hawaii, USA (Mobley & Herman, 1985; Smultea, 1994), the Virgin Banks and West Indies–Caribbean (Smith et al., 1999; Mattila et al., 1994), Mozambique (Findlay et al., 1994), Madagascar (Ersts & Rosenbaum, 2003) and Ecuador (Scheidat et al., 2000) which had 6.8% to 28% of groups with calves. In Abrolhos Bank, females with calves preferentially use shallower waters around the archipelago (Martins et al., 2001), probably to take advantage of calmer water, to minimize the possibility of predation by sharks, or to avoid harassment by males. Additionally, the Abrolhos Reef, which covers approximately one quarter of the study area, may act as protection from the prevailing winds that are from the north-east and south-east, making whale groups with calves concentrate in this region.

Among humpback groups without calves, DYAD and 1AD were more frequently observed than TRIO and TRIO+. These TRIO and TRIO+ were larger groups characterized by high levels of activity and are believed to be males competing for sexual access to a single mature female (Tyack & Whitehead, 1983). The predominance of females with calves using the area and that males prefer to associate with females without calves (Craig et al., 2002) most likely explains the lower proportion of TRIO and TRIO+ groups in this study area.

There are several hypotheses as to the function of the escort, but it is still not well understood. The escort of mother–calf pairs is thought to be a male seeking access to a female that comes into post-partum oestrus (e.g. Glockner-Ferrari & Ferrari, 1990). Although the probability of post-partum ovulation leading to successful conception is not high, escorting a female with a calf may be a male reproductive strategy that has some success (e.g. Glockner-Ferrari & Ferrari, 1985). Also as females without a calf become increasingly rare relative to females with a calf as the reproductive season progresses (Dawbin, 1966), males turn their attention to females with a calf (Craig et al., 2002). Our results showed that mother–calf accompanied by one or more escort became more frequent along the season, supporting the idea that males have an escort position in order to access a female with calf. However, in general we observed more MOC groups than MOCE groups, and even in the 'C' phase solitary mother and calf pairs were still frequently observed. It might be that the unusual equal sex ratio found in the Abrolhos Bank area (Engel, 2003) would cause fewer males to use this reproductive strategy because there would be sufficient numbers of non-lactating receptive females, which seems to lead to higher reproductive success (Craig et al., 2002).

Except for the 1AD category that appeared with mostly equal proportion in all phases, the proportion of the other humpback group categories did vary among the three phases of the season, where all groups with calves increased and groups without calves decreased as the season advanced. This temporal progression may reflect the segregated migration pattern observed for humpbacks, the change in the social status of individual whales during the season, and/or may reflect a mating and breeding strategy. It is known that females at the end of lactation are the first to leave feeding grounds, followed by immature individuals and then adults and pregnant females, which are the last to arrive on the breeding ground (Dawbin, 1966). The return to high latitude waters occurs in reverse order (Dawbin, 1966). So the groups of DYAD and TRIO observed in higher proportion at the beginning of the season may be immature individuals and adults of both sexes and females with yearlings. As the season progresses it is expected that the social status of these individuals changes. Whales form and leave competitive groups, pregnant females give birth and become MOC groups, newly pregnant females and females without a calf leave earlier to feeding grounds (e.g. Dawbin, 1966), and (as discussed earlier) later in the season mature males tend to associate with mother and calf groups (e.g. Herman & Antinoja, 1977; Glockner-Ferrari & Ferrari, 1985; Scheidat et al., 2000). Thus the TRIO+ category diminished while the MOCE+ category became proportionally more frequent, as Martins et al. (2001) reported for Abrolhos Bank.

Morete et al. (2003) reported a difference in the number of adult whales with time of day, where more whales were sighted during the morning period. This analysis did not find any evidence that group categories showed any preference to morning or afternoon in the archipelago's waters.

Although oscillations occurred, there was no statistical evidence that the relative proportion among group categories varied among the seven seasons studied. This humpback population is increasing in numbers (Freitas et al., 2004), so we can suggest that the increased number of whales did not affect the general pattern of group structure, at least around the Abrolhos Archipelago within the study period.

In conclusion, the proportion of humpback group categories observed around the Abrolhos Archipelago was similar to other breeding areas for those groups without calves (i.e. 1AD and DYAD). Competitive groups (MOCE+ and TRIO+) were present in lower proportions. The fact that solitary mother and calf pairs were still frequent towards the end of the season may be due to the equal sex ratio (Engel, 2003) in Abrolhos waters, leading to different dynamics of escorts toward mother and calf groups. Our major difference among other humpback breeding grounds was in respect of number of calves present. Probably, protection by the Abrolhos Reef from the prevailing winds makes the Abrolhos Archipelago preferred by groups with calves, making this area extremely important to the humpback whale. Therefore proper management is strongly recommended.

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