

## ORIGINAL ARTICLE

# A missing piece from a bigger puzzle: declining occurrence of a transient group of bottlenose dolphins off Southeastern Brazil

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## Abstract

Bottlenose dolphins are widespread off South America with patchy distributions throughout coastal, nearshore and offshore waters. Only limited information on the connectivity between individuals from these different habitats exists, despite the importance of understanding the overall population structure. A group of bottlenose dolphins in an insular habitat off Brazil may help provide evidence of the structure of a larger pelagic population in Brazilian waters. It is unknown whether the dolphins that use this habitat seasonally are part of an open population, a closed population of transient animals, or even individuals from offshore or nearshore groups. To explore the nature of these seasonal visitors we combined two strategies. First, by assessing the population parameters, we described a small group of individuals (maximum of 38 individuals in 2004 and five individuals in 2010) characterized by wide-ranging behavior, low survival probabilities (64%) and an apparent population decline. Secondly, by exploring their social organization at a fine scale, we observed that within a stable group, the dyadic associations are fluid and mostly of short duration, similar to well-known coastal bottlenose dolphin societies. The evidence of a non-structured social network seems to be coupled with apparent seasonal use of this insular protected area for calf rearing and/or reproductive strategies. Overall, our findings suggest that this group may not be an aggregation of individuals from different populations in a specific area, but a relatively stable group formed by the same animals. While continuing research efforts are necessary along the South America coast, the abandonment of the study area by this group may hamper the understanding of population structure and connectivity among pelagic and coastal populations of bottlenose dolphins, as well as the ecological and behavioral mechanisms driving their seasonal occurrence in oceanic habitats.

## Introduction

Small animal populations confined to localized geographic areas are often priorities for conservation purposes (Smith *et al.* 2006). Identifying these populations and their peculiarities is the first step for any strategy

focused on the mitigation of anthropogenic impacts (Currey *et al.* 2009). For cetacean species, however, the edges of a population unit are not always clear, making assessment efforts challenging (Thompson *et al.* 2000). One of the most studied cetacean species, the common bottlenose dolphin *Tursiops truncatus*, (hereafter bottlenose

dolphin) is well known for the behavioral plasticity among populations (Connor *et al.* 2000b). These diverse lifestyles are mirrored in the controversy over the taxonomic status of this genus (Möller *et al.* 2008), and generate many uncertainties about the nature of localized and transient groups throughout their global distribution. Indeed, long-term studies have revealed varying degrees of population structure (Natoli *et al.* 2008) and behavioral specialization in response to different habitat conditions (Segura *et al.* 2006).

Bottlenose dolphins are widespread, with an apparent patchy distribution throughout the South American coast. A few small, coastal and resident populations are found from Argentina to Southern Brazil (Simões-Lopes 1991; Laporta 2009; Vermeulen & Cammareri 2009; Fruet *et al.* 2011) but pelagic populations are still fairly unknown. These pelagic populations can be classified as offshore oceanic groups, while the coastal populations are considered inshore or nearshore groups (Sellas *et al.* 2013). Although a few inshore coastal populations have been monitored recently and their population parameters, social organization and foraging behaviors studied (*e.g.* Fruet *et al.* 2011; Daura-Jorge *et al.* 2012a,b), to date there is insufficient information on the population structure and levels of connectivity among them, as well as the role of unknown nearshore and offshore animals. At the regional scale, when considering these non-resident populations, the uncertainty is even higher, inevitably raising the following question: do these nearshore/offshore animals connect isolated and resident inshore populations of bottlenose dolphins? Genetic analysis may shed light on this query (Mirimin *et al.* 2011), but identifying and understanding the distribution patterns and behavioral processes of these non-residents or transient animals is a critical piece for assembling the puzzle of these different bottlenose dolphin populations.

Small groups of bottlenose dolphins are observed seasonally during the winter and spring close to the Cagarras Archipelago (CA), a sheltered coastal insular habitat off Brazil (Barbosa *et al.* 2008). This seasonal pattern of occurrence appears to differ from other insular populations, where animals from open populations are observed throughout the year (*e.g.* Bearzi *et al.* 1997; Shane 2004; Kerr *et al.* 2005; Oviedo & Silva 2005). The bottlenose dolphins we study here may provide clues for these questions and allow us to better assess the regional conservation status of this species. In general, these insular populations are composed of several geographic communities that interact with neighboring communities and with transient dolphins (Quérouil *et al.* 2007; Silva *et al.* 2009). Despite the seasonal pattern, individual identification efforts suggest that these seasonal visitors of CA are always the same animals of unknown origin (Lodi &

Monteiro-Neto 2012). Therefore, it is not trivial to identify the ecological nature of these groups: whether they are from an open population, a closed population of transient animals, or even from inshore, nearshore or offshore groups. In all cases, it seems that the seasonal use of the CA is linked with vital behaviors, such as socialization and calf rearing (Lodi 2009).

Since this pattern of small transient groups is recurrent yet still unexplored throughout the South and Southeast Brazilian coast (Fruet *et al.* 2011; Daura-Jorge *et al.* 2012a), understanding their dynamic may allow us to better understand these multiple coastal bottlenose dolphin populations and/or the longitudinal patterns of distribution. We combined two strategies to comprehend the seasonal visits of bottlenose dolphin in the CA. First, we assessed population parameters such as population size and survival probabilities to characterize the population unit and examined population trends. Two possible outcomes were expected: these animals are (i) part of a superpopulation of multiple populations units with nearshore habits, wide-ranging behavior and transient movement patterns that meet in the study area or (ii) a transient coastal population unit with no resident pattern, but with high site fidelity in specific areas for key behaviors. Secondly, we characterized the social organization of these groups to infer the behavioral and ecological functions behind the seasonal use of this coastal insular habitat.

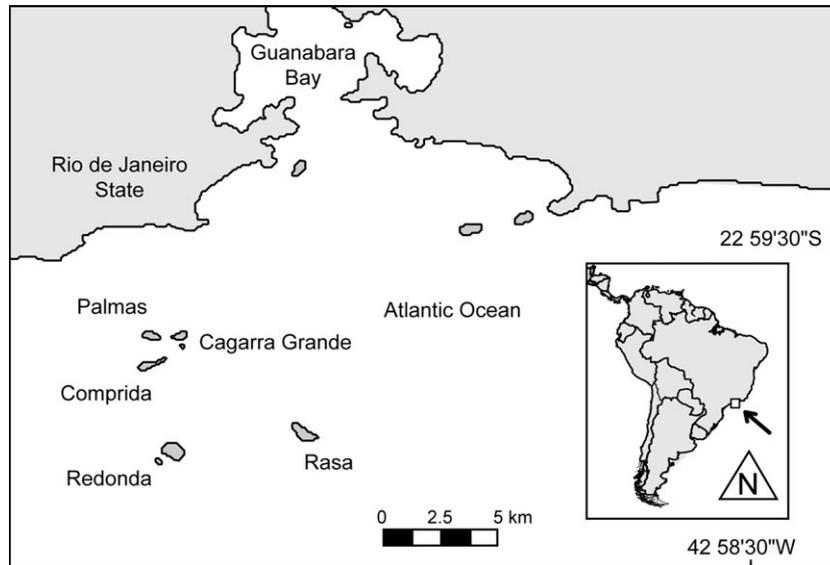
## Material and Methods

### Study area

The Cagarras Archipelago (23°01' S, 043°12' W to 23°03' S, 43°12' W) is a nearshore group of islands (das Palmas, Cagarras Grande and Comprida), three small islets and seven rocky outcrops (Fig. 1). The total inner area of the archipelago is approximately 2.39 km<sup>2</sup> and the average water depth varies between 2 and 18 m (Nautical Chart No. 1501, Directorate of Hydrography and Navigation of the Navy of Brazil). In April 2010, a marine protected area, the *Monumento Natural do Arquipélago das Ilhas Cagarras*, was created by Federal Law no. 12229.

### Sampling protocol

We conducted weekly boat-based surveys from 9:00 to 15:00 h in favorable weather (Beaufort scale  $\leq 2$ ) between 2004 and 2012 (August to November in 2004, 2006 and 2010, August to October in 2007, 2008 and 2009 and August to December in 2011 and 2012). Since bottlenose dolphins are present in the Cagarras Archipelago during austral winter and spring (Barbosa *et al.* 2008), the sampling effort was concentrated in these seasons; however,



**Fig. 1.** Cagarra Archipelago, Southeastern Brazil, and the main islands: Palmas, Cagarra Grande and Comprida.

we conducted some surveys in other seasons to confirm this seasonal pattern. Search efforts focused on the interior of the insular complex and aimed to cover this area homogeneously (Fig. 1). For all surveys, dolphins were already present in the inner area of the archipelago when we arrived and remained there until we left. We also conducted daily surveys in adjacent areas (radius of 1 km) of the archipelago but no dolphins were sighted.

A group was defined as all dolphins observed in the sheltered inner area of the archipelago. The group was then classified into subgroups using two criteria: (i) behavior - animals moving in the same direction and performing coordinated and synchronic activities at the water surface; (ii) physical proximity - the distance between members of the subgroup not exceeding two body-lengths (adapted from Quintana-Rizzo & Wells 2001; Whitehead 2008b). We used digital videography to identify individuals based on their dorsal fins (see below). The dorsal fins of all subgroups were recorded, beginning with a randomly selected subgroup and proceeding to the closest subgroup until the entire group was recorded with digital video. The engines of the boat were turned off during observations and no behavioral response was noticed.

We classified the genders of adults (approximately  $\geq 3$  m in length) using the following criteria: (i) possible females - adults exhibiting consistent and synchronous associations with neonates and calves (animals one-third and one-half of adult size, respectively), and (ii) possible males - large size, with many body marks and scratches, and never accompanied by neonates or calves (cf. Bearzi *et al.* 1997; Quintana-Rizzo & Wells 2001; Shane 2004). Since there is uncertainty associated with this gender classification, we did not include gender in the mark-recapture analysis.

#### Individual identification

Individuals were identified based on the profile shape of their dorsal fins and on the presence of nicks and scars, using the video identification technique proposed by Lodi *et al.* (2009). The best photograph of each individual (selected as the frame in which the dorsal fin was in focus and perpendicular to the camera) from each occasion was compared with the best photographs taken of previously identified individuals. Each unambiguous match was considered a resighting. From this procedure, we built the resighting history of marked individuals. Unmarked animals were also recorded. Similarly to mark-recapture methods, mark-resight analyses assume that marked and unmarked (see details below) animals are identified correctly. Misidentifications due to poor quality photographs or changes in natural marks can lead to positively biased estimates of abundance (Link *et al.* 2010). To avoid or reduce the chance of a misidentification, no calves, animals with temporary marks or poor images were included in our population analysis. For the social analysis, we analysed only the 19 adult individuals (of 22) that were sighted on three or more days per year to increase precision in association indices (Whitehead 2008b). This less restrictive observation threshold was intentionally applied to consider possible transient individuals (*e.g.* Wolf *et al.* 2007; Cantor *et al.* 2012b).

#### Mark-resight analysis

Mark-resight histories for all identified dolphins were analysed using the program MARK (White 2008). We applied the Poisson-log normal mark-resight model, which is appropriate when the exact number of marked

animals is not known (McClintock *et al.* 2009). This analysis incorporates additional data on the number of unmarked individuals. Therefore, the usual *a posteriori* correction in the abundance estimates to account for the proportion of unmarked individuals (*e.g.* Silva *et al.* 2009; Cantor *et al.* 2012a) is not necessary. A key assumption for this procedure is that marked individuals are representative of the population in terms of sighting probabilities. To include unmarked individuals in the modeling procedure, we used the total number of unidentifiable dolphins observed during all occasions of a primary period (defined here as each year). The Poisson-log normal model is also recommended when each primary period is assumed to be closed (McClintock & White 2009) because this model is able to deal with variation in sighting probability due to individual heterogeneity caused by physical or behavioral differences between animals. It is useful when analysing small cetacean datasets, which are commonly affected by individual heterogeneity or even by geographic or demographic closure violation (Hammond *et al.* 1990). When applied under the robust design procedure (as conducted here) the Poisson-log normal model also deals with variation in sighting probability over time.

Using this analytical procedure, we estimated the number of unmarked dolphins for each primary period ( $U$ ), the mean resighting probability for each primary period ( $\alpha$ ) in a log-scale, the variation promoted by individual heterogeneity ( $\sigma$ ), the apparent survival probability ( $\phi$ ), and the transition rates from observable and unobservable states, given an individual was not present to be observed ( $y''$  = the probability of transitioning from an observable to an unobservable state between primary periods given an individual was present to be observed;  $y'$  = the probability of remaining in an unobservable state). For the Poisson-log normal model, abundance estimates were derived from the estimated number of sightings of unmarked individuals and the overall mean resighting rate, together with the total number of times marked individuals were resighted one or more times. We are confident in our estimates of unmarked dolphins because group sizes were small and there were only a small number of individuals.

We built a set of models including or excluding time-dependence and individual heterogeneity as parameters. The number of unmarked individuals ( $U$ ) was modeled as always assuming variance between primary periods (time-dependent,  $t$ ). Resighting probability was modeled as constant or varying across years ( $\alpha$ ). Individual heterogeneity ( $\sigma$ ) was also modeled as constant or time-dependent ( $t$ ), or fixed to zero to remove this effect. Survival probabilities ( $\phi$ ) were also modeled as constant or as a function time  $t$  (years). Transition rates were modeled as

a function of time and as constant and we also built a model where  $y'' = y'$ . We modeled all combinations of parameter conditions (a total of 19 models) and presented the results of the most reliable models. Some models (not presented) were likely confounded by overparameterization. Model selection used Akaike's information criterion (AIC) values produced by MARK, taking into account differences in effective sample size and lack of fit (AICc) (Burnham & Anderson 2002). Although we did not test for the assumption of closure within primary periods, this is a biologically reasonable assumption since we found a high encounter rate and resighting rate of a small number of dolphins.

Considering the small group of seasonal visitors or residents in the area, we also presented the estimates from the POPAN open model parameterization (Schwarz & Arnason 1996) to compare the annual abundance estimates with the total abundance estimated. Here we did not include the unmarked individuals in the abundance estimates, and used the abundance of marked dolphins to examine the possibility that this group is part of a larger super-population (*sensu* Schwarz & Arnason 1996) moving throughout a more extensive geographic area. To run the open model, we pooled each year period as a single occasion and modeled the survival probability ( $\phi$ ), capture probabilities ( $p$ ) and probability of entrance ( $pent$ ) as a function or not of time. Only the most parsimonious model (also selected by AICc) with its abundance estimates was chosen. For this open population approach we evaluated overdispersion, a common feature for cetacean data due to the violation of assumptions of equal capture probability or equal survival probabilities. To examine this extra binomial variation, we estimated  $\hat{c}$  by dividing the chi-square statistics of goodness of fit tests by the number of degree of freedom. The  $\hat{c}$  value was used to adjust the lack of fit of the models.

### Social interactions

Individuals found in the same subgroup in a given day were considered associated (adapted from Whitehead & Dufault 1999). Dyadic associations were quantified by the half-weight index (HWI; Cairns & Schawager 1987), an estimate of the proportion of time a pair of individuals was observed in the same subgroup in a given day, in relation to the amount of time they were observed in different subgroups (Whitehead & Dufault 1999). This index compensates for bias when not all individuals in a subgroup can be identified, or when individuals are more likely to be identified when not associated (Whitehead 2008b). Association values were grouped into the following association categories: low ( $HWI \leq 0.2$ ), moderately low ( $0.2 < HWI \leq 0.4$ ), moderate ( $0.4 < HWI \leq 0.6$ ),

moderately high ( $0.6 < \text{HWI} \leq 0.8$ ) and high ( $\text{HWI} > 0.8$ ) (Quintana-Rizzo & Wells 2001). To estimate the accuracy of the association matrix, we correlated the true and the estimated association matrices using the maximum likelihood method (Whitehead 2008a). This is a measure of how well the association matrix reflects the real social structure. A correlation of about 0.4 indicates a somewhat representative pattern, whereas values around 0.8 are considered good representations (cf. Whitehead 2008a). The coefficient of variation of association indices (S, Social differentiation) was evaluated by the maximum likelihood method (Whitehead 2008a).

### Testing association patterns

To test the null hypothesis that individuals associate randomly, we performed a Monte Carlo simulation (Bejder *et al.* 1998) permuting subgroups within sampling periods (Whitehead 1999). To ensure independence of permuted matrices, we performed 20,000 iterations (Bejder *et al.* 1998) with 1000 flips ('checkerboard swaps') per iteration (cf. Miklós & Podani 2004). This test also enables the identification of short- and long-term preferred associations (Bejder *et al.* 1998). A mean observed HWI that is lower than the null expectation indicates the occurrence of short-term preferences (within sampling periods). An observed HWI coefficient of variation (CV) that is significantly higher than the CV expected by chance is evidence of preferred long-term associations (between sampling periods) (Whitehead 1999, 2008b; Whitehead *et al.* 2005). The P-value is the proportion of random values higher than the observed data, and a significant difference was indicated by P-values larger than  $>0.95$  (cf. Whitehead 1999; Whitehead *et al.* 2005).

### Association temporal patterns

Standardized lagged association rates (SLAR) analysis was used to examine the stability of relationships over time (Whitehead 1995). This procedure estimates the probability  $g'(d)$  that a previously associated pair of individuals will be found in the same subgroup after a given time lag  $t$  (Whitehead 1995, 2008b). As a benchmark, we calculated the standardized null association rate (SNAR): the expected LAR values if individuals associate at random. Precision of SLAR and SNAR, represented by standard errors, was estimated by the Jackknife procedure (1000 replications omitting 30 sampling periods each time) (Whitehead 2008b). To avoid potential biases, these analyses were performed without the data restriction of five resightings (cf. Whitehead 1995).

Four candidate exponential decay models were fitted to the observed data to estimate structural parameters of the

social organization (Whitehead 1995). They are based on the combination of two potential components of societies with fission–fusion dynamics: (i) constant companions, in which pairs associate permanently, and (ii) casual acquaintances, in which pairs associate for some time (more than one sampling period), disassociate, and re-associate (see Whitehead 1995, 2008b). The most parsimonious model was selected based on the quasi Akaike's information criterion (QAICc) (Burnham & Anderson 2002; Whitehead 2007). All analyses were performed using the compiled version of SOCPROG 2.4 software (Whitehead 2009).

### Social network

The association matrix was plotted as a social network depicting individuals (nodes) connected by edges whose thickness is proportional to the association index (Boccalletti *et al.* 2006). The social network topology was described by three metrics: density, weighted global clustering coefficient and modularity:

*Density* is a measure of the network connectivity, representing the proportion of realized interactions in relation to all possible interactions between the individuals.

*Global clustering coefficient* quantifies the overall tendency of nodes to cluster together in a network. It represents the chance of individuals  $a$  and  $b$  being associated with each other, if both are also associated with an individual  $c$ . To take edge weights into account, the associations were standardized by the average value in a triplet (see Opsahl & Panzarasa 2009).

*Modularity* calculates the individuals' tendency to cluster in cohesive subgraphs. A modular network topology would then be arranged into weakly interlinked groups of nodes, which are strongly internally connected. Modularity was assessed calculating the metric  $Q$  with the modularity matrix technique. The most parsimonious split in the network maximizes the weights of edges within modules and minimizes the weights of edges between modules (Newman 2006).  $Q$ -values higher than 0.3 indicate a reliable network partition in modules (see Newman 2006; Whitehead 2008b, 2009). Network analyses were carried out in R environment (R Core Team, 2011) using *tnet* package (Opsahl 2009) and SOCPROG (Whitehead 2009).

### Results

To examine population dynamics, we analysed data collected from 65 field expeditions conducted in 2004 and 2006–2010 because no individuals were resighted in 2011 and 2012, despite increased the sampling effort (Table 1). A total of 229 h of effective observations of *T. truncatus*

**Table 1.** Summary of annual sampling effort and basic results of the mark–recapture and social organization study with bottlenose dolphins in the Cagaras Archipelago, Brazil.

Year	Number of surveys	Sampling effort (min)	Total groups	Sighted groups per survey	Mean number of identified dolphins $\pm$ SD	Mean number of immatures $\pm$ SD	Mean group size $\pm$ SD	Group size range
2004	11	3960	11	1	11.5 $\pm$ 0.7	7.8 $\pm$ 2.3	21.4 $\pm$ 3.3	18–30
2006	12	2659	12	1	11 $\pm$ 2.4	5.8 $\pm$ 1.4	17.3 $\pm$ 1.5	15–19
2007	10	2108	10	1	10.7 $\pm$ 2.6	5.9 $\pm$ 1.3	16.6 $\pm$ 3.6	10–21
2008	10	2015	9	0.9	4.5 $\pm$ 0.8	0	4.4 $\pm$ 0.8	3–5
2009	11	2678	4	0.4	5.5 $\pm$ 1.7	5.5 $\pm$ 1.7	5.5 $\pm$ 1.7	4–7
2010	11	2542	5	0.4	3 $\pm$ 0	1.6 $\pm$ 0.5	5	5
2011	20	5560	0	0	0	0	–	–
2012	21	4560	0	0	0	0	–	–

were made. The individual identification data were collected on 29 h 41 min of digital videotape, of which 8 h 02 min (27.2%) contained useful information (see Table 1). For the social analyses, we focused on 31 field expeditions carried out from August to November in 2006 and August to October in 2007 and 2008, representing 113 h of effective observation of the dolphins. The associated data were collected on 10 h 21 min of digital tape videos, of which 3 h (29.3%) contained useful information.

#### Mark–resight estimates

The most parsimonious mark–resight model (Table 2) yielded three important outcomes: (i) the mean resighting probability varied between primary periods ( $\alpha_t$ ); (ii) there was an additional variation from individual heterogeneity, which was also constant between primary periods ( $\sigma$ ); and (iii) the number of unmarked individuals varied

between primary periods ( $U_t$ ). Additionally, we found a constant apparent survival probability ( $\phi$ ) and that the probability of transitioning to an unobservable state between primary periods ( $y''$ ) was the same as the probability of remaining unobservable ( $y'$ ). Since the first four models supported the data (Table 2), we used model averaging to calculate the abundance estimates.

#### Resighting rates, survival and transition

As shown by the top-ranked model (Table 2), resighting rates varied between years from 2.66 (SE = 0.76; 95% CI = 1.53–4.64) in 2008 to 7.16 (SE = 0.69; 95% CI = 5.91–8.66) in 2006, without a clear time trend. Although the model indicated individual heterogeneity ( $\sigma$ ), it was low and close to zero (0.16; SE = 0.09; 95% CI = 0.05–0.46). Apparent survival was also constant and low for the species (0.64; SE = 0.06; 95% CI = 0.51–0.75). The probability of transitioning to an unobservable state (out

**Table 2.** Mark–resight models ranked by the lowest Akaike information criterion (AICc) applied to the 2004–2006/2010 video identification dataset of bottlenose dolphins in the Cagaras Archipelago. For each model we showed the adjusted AICc values, the delta AICc, the AICc weight, the model likelihood, and the number of parameters. The following parameters were included in the models: mean resighting rate ( $\alpha$ ), individual heterogeneity ( $\sigma$ ), number of unmarked individuals ( $U$ ), apparent survival ( $\phi$ ), probability of transitioning from an observable state in one season to an unobservable state in the next season ( $y''$ ), probability of remaining in an unobservable state in the next season when in an unobservable state in the previous season ( $y'$ ). Time-dependence was indicated by the presence of 't' after each parameter.

Model	AICc	$\Delta$ AICc	AICc weights	Model likelihood	No. of parameters
1	{ $\alpha(t) \sigma(\cdot) U(t) \phi(\cdot) y''(\cdot) = y'(\cdot)$ }	511.97	0	0.3571	15
2	{ $\alpha(\cdot) \sigma(\cdot) U(t) \phi(\cdot) y''(\cdot) = y'(\cdot)$ }	511.97	0.008	0.3556	10
3	{ $\alpha(\cdot) \sigma(0) U(t) \phi(\cdot) y''(\cdot) = y'(\cdot)$ }	512.73	0.761	0.1481	9
4	{ $\alpha(\cdot) \sigma(\cdot) U(t) \phi(\cdot) y''(\cdot) y'(\cdot)$ }	512.99	1.026	0.1296	11
5	{ $\alpha(\cdot) \sigma(t) U(t) \phi(\cdot) y''(\cdot) = y'(\cdot)$ }	520.18	8.214	0.0036	15
6	{ $\alpha(\cdot) \sigma(\cdot) U(t) \phi(\cdot) y''(t) y'(t)$ }	520.32	8.353	0.0033	15
7	{ $\alpha(\cdot) \sigma(\cdot) U(t) \phi(\cdot) y''(\cdot) y'(t)$ }	521.0	9.030	0.0024	14
8	{ $\alpha(t) \sigma(t) U(t) \phi(\cdot) y''(\cdot) = y'(\cdot)$ }	525.86	13.889	0.0002	20
9	{ $\alpha(\cdot) \sigma(\cdot) U(t) \phi(\cdot) y''(t) y'(t)$ }	528.27	16.304	0	18
10	{ $\alpha(t) \sigma(\cdot) U(t) \phi(\cdot) y''(t) y'(t)$ }	533.30	21.329	0	23
11	{ $\alpha(t) \sigma(t) U(t) \phi(\cdot) y''(t) y'(t)$ }	554.83	42.862	0	28
12	{ $\alpha(t) \sigma(t) U(t) \phi(t) y''(t) y'(t)$ }	578.50	66.530	0	32

of the study area) was modeled as being equal ( $y'' = y'$ ) to the probability of remaining in an unobservable state (out of the study area). Both were constant between years and were estimated as 0.16 (SE = 0.07; 95%CI = 0.06–0.36). These transitioning values combined with the low survival probabilities are consistent with the clear downward trend in abundance estimates shown below.

### Abundances

The number of unmarked individuals (U) estimated by the most parsimonious model varied from 18 (SE = 2.63; 95%CI = 14.16–24.57) in 2004 to only one in 2008. Based on the average of the four most parsimonious models, the abundance estimates varied from a maximum of 38 individuals in 2004 (SE = 2.33; 95%CI = 33–42) to a minimum of five individuals in 2010 (SE = 0.65; 95%CI = 3–6) (see Table 3), showing a clear negative trend across time until 2011 and 2012, when the dolphins completely disappeared from the study area. Abundance estimates from the most parsimonious model of the POPAN approach [a null model for survival and capture probabilities –  $\phi(i) p(.) pent(t)$ ] were consistent with the negative trend observed by mark–resight models but also showed a slight difference between the higher estimate for 2004 (22, SE = 2.89; 95%CI = 16.36–27.69) and the total number of animals that used the area throughout the study (32, SE = 1.09; 95%CI = 30.03–34.32).

### Social structure

We recorded 709 events of associations between 19 bottlenose dolphins. The gender of seven individuals was assigned (five possible females – AC#12, #17, #18, #21, #24, and two males – AC#01 and #22). The estimated association matrix was a good representation of the true pattern ( $r = 0.90 \pm 0.04$ ). The HWI varied between 0.0

and 0.86 (mean =  $0.38 \pm 0.18$ ; median = 0.36). Mean HWI of female pairs was  $0.39 \pm 0.04$  SD and the pair of males (AC#01–22) showed HWI = 0.73. The moderately low HWI (ranging from 0.2 to 0.4, mean =  $0.31 \pm 0.06$ ) were most representative of the population (Fig. 2). The individuals AC#22, #01 and #13 presented the highest mean HWI values (0.47, 0.46, 0.46, respectively) and animals AC#13 and #12 exhibited the highest association (HWI = 0.86).

The null hypothesis that individuals associate randomly was not rejected. We found no evidence of preferences in long-term (observed HWI CV = 0.465 significantly lower than the random HWI CV = 0.497,  $P = 0.009$ ) or short-term associations (observed mean HWI = 0.381 not different than mean random HWI = 0.378,  $P = 0.772$ ). No pair of dolphins showed a significant value of HWI. The average number of identifications per individual ( $H = 93.3$ ), combined with the variation of association indices ( $S = 0.572 \pm 0.04$ ), conferred a sufficient power to the test for social preference ( $S^2 \cdot H = 53.4 > 5$ , cf. Whitehead 2008a).

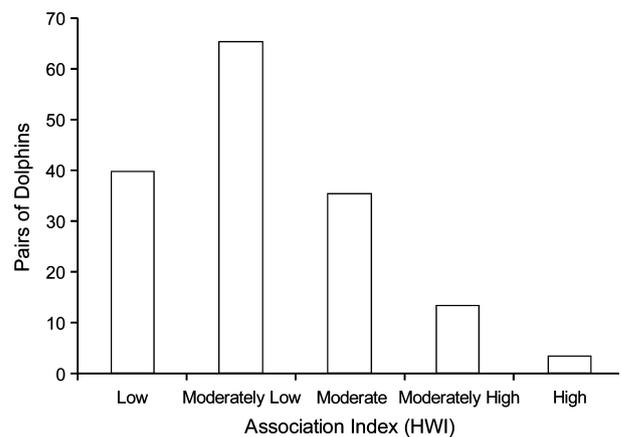
The most parsimonious model for temporal stability of associations (Table 4) suggests the existence of casual acquaintances, indicating that associations were mostly of short duration. SLARs were higher than the null expectation (SNAR) until a short period of about 30 days, after which the probabilities of pairs remaining associated was indistinguishable from the null expectation (Fig. 3).

The social network was composed of  $n = 19$  nodes, representing individuals, connected by 139 weighted edges (Fig. 4). Regarding the maximum number of edges [ $n*(n-1)/2 = 171$ ], the density of interactions was high ( $d = 0.813$ ). The global clustering coefficient ( $C_w$ ,  $am = 0.906$ ) was also high. These results indicated quite a

**Table 3.** Abundance estimates (N), the associated standard errors (SE) and 95 percent confidence intervals (95%CI) from the most parsimonious mark–resighting and POPAN models applied to the 2004–2006/2010 video identification dataset of bottlenose dolphins in the Cagarras Archipelago. No dolphins were sighted in 2011 or 2012.

Year	Mark–resight estimates			POPAN estimates		
	N	SE	95%CI	N*	SE	95%CI
2004	38	2.33	33–42	22	2.89	16–27
2006	29	1.66	25–32	16	2.27	12–21
2007	23	1.44	20–26	13	2.25	9–18
2008	7	0.29	6–8	10	2.21	6–15
2009	7	0.83	4–10	7	2.05	3–11
2010	4	0.65	3–6	5	1.81	2–9

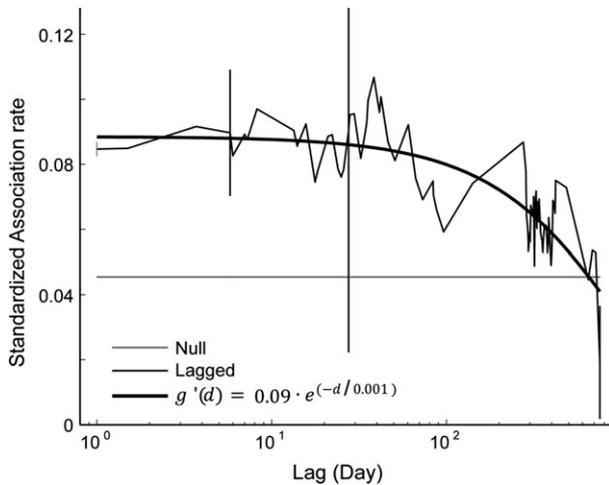
\*Only marked individuals.



**Fig. 2.** Associations (half-weight index) of all pairs of bottlenose dolphins in the Cagarras Archipelago ( $n = 171$ ), according to the categories described in the text (cf. Quintana-Rizzo & Wells 2001).

**Table 4.** Exponential decay models ranked by lowest QAICc for standardized lagged association rates (SLAR) of the bottlenose dolphins from Cagarras Archipelago between 2006 and 2008. For details on the parameters of the models, see Whitehead (1995, 2008b).

SLAR models	Model interpretation	QAICc	$\Delta$ QAICc
$g'(d) = a_2 \cdot e^{-a_1 \cdot d}$	Casual acquaintances	28086.5	0
$g'(d) = a_3 \cdot e^{-a_1 \cdot d} + a_4 \cdot e^{-a_2 \cdot d}$	Two levels of casual acquaintances	28090.2	3.7
$g'(d) = a_2 + a_3 \cdot e^{-a_1 \cdot d}$	Constant companions + casual acquaintances	28235.4	148.9
$g'(d) = a_1$	Constant companions	28235.6	149.1

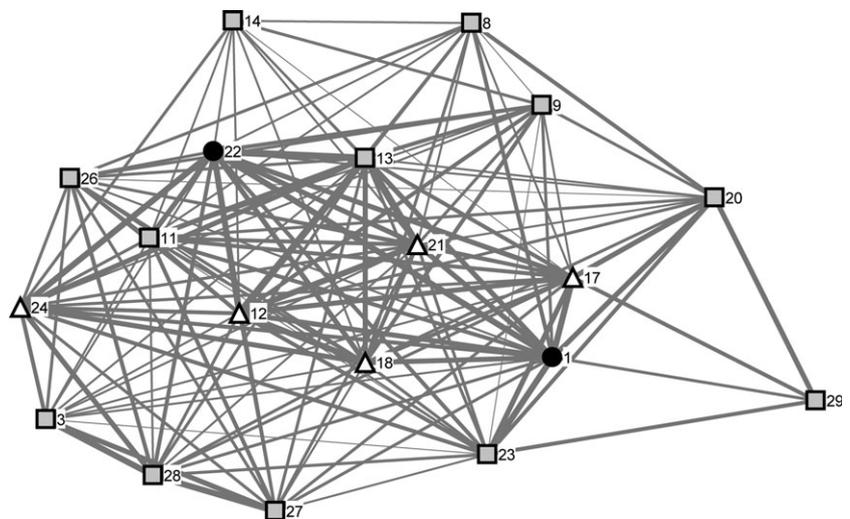
**Fig. 3.** Standardized lagged association Rates (black line) and the standardized null association rates (gray line) of the bottlenose dolphins from Cagarras Archipelago between 2006 and 2008. Vertical lines represent the standard error. The thicker black line represents the best-fit model.

connected network. The modularity was very low ( $Q_{\max} = 0.136$ ;  $Q_{\max} < 0.3$ ) and did not suggest any reliable division of the network into modules.

## Discussion

Our combined analytical approach offers insights into the nature of the population and social dynamics of the bottlenose dolphins that seasonally visit the Cagarras Archipelago. Our findings suggest that this group of dolphins is relatively stable, but within which individuals associate randomly, and not part of a larger and overspread population, but a transient small population unit.

To date there is only one annual survival probability estimated for bottlenose dolphins on the South American coast ( $\phi = 0.91$ , see Daura-Jorge *et al.* 2012a), which is markedly higher than the survival estimates we present here ( $\phi = 0.64$ ). Indeed, the apparent survival rate presented here is among the lowest of estimates for bottlenose dolphins worldwide (Fortuna 2006; Currey *et al.* 2008; Silva *et al.* 2009; Mansur *et al.* 2012). Such a low survival probability could represent both a gradual abandonment of the study area or a high mortality outside this area. The transitioning probabilities from observed to unobserved states together with the probability of remaining in an unobservable state (16%) suggest a wide-ranging behavioral pattern of occasional visitors. Indeed, at least eight animals in our capture-history were sighted 100 km southwest of our study area (Lodi *et al.* 2008),

**Fig. 4.** Social network of the 19 bottlenose dolphins from Cagarras Archipelago between 2006 and 2008 (triangle = possible females, circles = possible males, squares = unidentified gender) displaying no obvious modular structure and a high density of connections. The network was plotted using NETDRAW 2.083 (Borgatti 2002, NetDraw: Graph visualization software, Harvard, Analytic Technologies).

and such wide-ranging behavior is not uncommon for coastal bottlenose dolphins without a well-defined resident area (Currey *et al.* 2009; Mansur *et al.* 2012) or for insular dolphins belonging to open populations which span several geographic communities (Silva *et al.* 2009). Interestingly, a peculiarity of this group is the seasonality in the movement of animals throughout the study area, a temporal pattern only observed in a few other coastal bottlenose dolphin populations (Ingram & Rogan 2002; Currey *et al.* 2009) that is generally linked with the local resource availability. Overall, this wide-ranging pattern would suggest that the individuals within this group are part of a larger super-population using a more extensive geographic region.

However, the additional population parameters allow us to propose alternative hypotheses. First, the abundance estimates yielded by the mark–resight models indicate a small population. More importantly, the estimates clearly follow a negative trend during our study period, declining to a critical number of only three adult dolphins identified in 2010, and finally to no observed visitors in 2011 and 2012. The negative abundance trend was corroborated by the POPAN method, which used only marked dolphins. In addition to the declining annual abundance estimates, the total abundance generated by the POPAN approach was not much higher than the highest annual abundance, which clearly suggests that it was always the same animals using the study area, with the few changes likely the result of infrequent birth and death events. This weakens our first hypothesis that a super-population, composed of different animals from different populations, is the source of individuals of this group. Instead, we propose that a relatively stable group, comprising individuals who are almost always together, has seasonally been using the area for specific purposes (*e.g.* nursery, calf-rearing) (Lodi & Monteiro-Neto 2012).

Although a few studies have identified transient groups in insular habitats (*i.e.* Silva *et al.* 2009), the nature of such groups is not well understood, especially in social terms. Our next step towards better understanding this unique group of bottlenose dolphins was to examine their social structure. Despite the apparent temporal stability of these animals as a social unit (one single group visiting the area), our findings suggest that within this group, the fission–fusion dynamics, which confer fluidity to many *T. truncatus* societies (*e.g.* Félix 1997; Quintana-Rizzo & Wells 2001; Vermeulen & Cammareri 2009) are operating. The group that used the Cagarras Archipelago did not demonstrate long- or short-term preferential associations, *i.e.* all members associate equally in temporary sub-groups. Moreover, the grouping pattern was characterized by casual acquaintances (*i.e.* associations that last for more than a day and then disassociate) indicating that

most dyadic associations were of short duration. Such ephemeral and random association patterns were then reflected into a dense and highly clustered network with no division in social modules, a plausible and expected topology given the small spatial scale studied (see Cantor *et al.* 2012b). Although it is not known whether the social patterns of non-coastal populations differ from those inshore, the particular low social stability among individuals within a stable social unit provides novel insights into the use of this coastal insular area. These social dynamics are the result of the combination of a small stable unit and the seasonal use of a restricted area, an atypical pattern for this species (but see Eisfeld & Robinson 2004).

The genus *Tursiops* exhibits a wide repertoire of social and reproductive strategies within and among populations (Connor *et al.* 2000a,b). The high number of immature individuals (mean =  $5.5 \pm 2.6$  SD of neonates, calves and juveniles) relative to the total group size suggests that the archipelago might be used during a particular time of the year as a nursery and/or calf-rearing area (Lodi 2009; Lodi & Monteiro-Neto 2012). This random association patterns might be explained by a promiscuous reproductive strategy during a specific period/area. Random association patterns in possible rearing areas have been recently suggested for other bottlenose dolphin populations (*e.g.* Vermeulen & Cammareri 2009). This strategy may ensure the benefits of group living (reduced predation risk; increased access to food resource, maternal care, learning abilities; Gibson & Mann 2008) during a reproductive period in a small and protected area like the Cagarras Archipelago. Although our findings suggest the use of this area for calf-rearing, in the future one should explore other reasons for the occurrence of bottlenose dolphins in the area. For instance, the relatively frequent feeding behavior (Barbosa *et al.* 2008; Lodi 2009) suggests that seasonal availability of resources, and thus good foraging habitat, may be a complementary mechanism.

## Conclusions

Although it would appear reasonable that the bottlenose dolphins using the Cagarras Archipelago could be part of a super-population formed by multiple populations, group stability suggests that all animals may have the same origin, belonging to the same transient population unit. Furthermore, the high degree of social flexibility observed within the group is consistent with the social patterns of well-studied inshore populations. Therefore, our findings suggest that this group is not an aggregation of individuals from different populations in a specific area. Rather, our data support the hypothesis that this group is a relatively stable group formed by the same

animals with transient and coastal habits, with no resident pattern, but with high site-fidelity in specific areas for specific purposes such as calf-rearing.

Understanding the nature of this bottlenose dolphin population unit clearly demands continued research efforts. The decline in observations of our studied population unit, followed by its disappearance in 2011, suggests the following non-exclusive possibilities: (i) the inner area of the Cagarras Archipelago has become less suitable for calf-rearing; (ii) other adjacent areas became more attractive; (iii) unknown threats over a large geographical area have caused a recent high mortality rate. At present, the available information on local threats, such as overfishing, organic pollution from adjacent land activities and intense boat traffic (see Lodi & Monteiro-Neto 2012 and references therein), would suggest that the Cagarras Archipelago may no longer attract these visitors. Further investigation should identify whether the low survival probability observed here is the result of true mortality or individuals remaining in an unobservable state (moving out of the study area or never returning).

Long-term monitoring of nearshore, insular and off-shore cetaceans inherently involves many logistical constraints. The seasonal occurrence of the small population unit studied here adds challenges for defining both ecological processes driving this population and management strategies. If continued monitoring finds individuals do not return to this area, we may have lost a key element in understanding the population structure and connectivity among pelagic and coastal populations of bottlenose dolphins, as well as the ecological and behavioral mechanisms driving the seasonal occurrence in insular habitats. In terms of management actions, small population units should be the targets of conservation plans. However, the apparent wide-ranging behavior of these dolphins makes it difficult to develop effective conservation strategies. In this case, protection of the area where they perform key behavior such as calf-rearing should remain a priority to maximize our chances of success. The Cagarras Archipelago is part of a Marine Protect Area, but the apparent disappearance of these animals calls for effective management practices that regulate the multiple local human activities such as overfishing, massive boat traffic and pollution.

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