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Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study

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ABSTRACT

This study represents the first attempt to study the population dynamics of Guiana dolphins (*Sotalia guianensis*), by evaluating a set of demographic parameters. The population of the Caravelas River estuary, eastern Brazil, was systematically monitored through a long-term mark-recapture experiment (2002–2009). Abundance estimates revealed a small population (57–124 dolphins), comprised of resident dolphins and individuals that temporarily leave or pass through the study area. Temporary emigration from the estuary to adjacencies ($\gamma'' = 0.33 \pm 0.07$ SE) and return rate ($1 - \gamma' = 0.67$) were moderate and constant, indicating that some dolphins use larger areas. Survival rate ($\varphi = 0.88 \pm 0.07$ SE) and abundance were constant throughout the study period. Power analysis showed that the current monitoring effort has high probability of detecting abrupt population declines ($1 - \beta = 0.9$). Although the monitoring is not yet sensitive to subtle population trends, sufficient time to identify them is feasible (additional 3 yr). Despite such apparent stability, this population, as many others, inhabits waters exposed to multiple human-related threats. Open and closed population modeling applied to photo-identification data provide a robust baseline for estimating several demographic parameters and can be applied to other populations to allow further comparisons. Such synergistic efforts will allow a reliable definition of conservation status of this species.

Key words: population dynamics, mark-recapture models, temporary emigration, survival, abundance, population trends, robust design, *Sotalia guianensis*, Abrolhos Bank.

Mark-recapture surveys are commonly used to estimate demographic parameters of several vertebrate taxa, including marine mammals (*e.g.*, Schaub *et al.* 2001; Bjørndal *et al.* 2003; Bradshaw *et al.* 2003, 2007; Bailey *et al.* 2004; Converse *et al.* 2006). Classically, abundance has been estimated through closed population modeling (Otis *et al.* 1978), which assumes a static population. The more realistic open population models account for temporal changes in population size as a balance between birth-immigration and death-emigration (Lebreton *et al.* 1992), chiefly to estimate survival rates. By using a combination of both approaches, it is possible to accurately estimate abundance from closed models and survival rate from open models (Pollock 1982). Additionally, the probability of temporary emigration can be addressed based on the fact that a given individual could be unavailable for capture at any time during the study (Kendall *et al.* 1997).

Detailed knowledge of the dynamics of most marine mammal populations is still incomplete. Logistical constraints mean that studying free-ranging cetaceans can be challenging, expensive, and time-consuming (see Taylor and Gerrodette 1993). As a consequence, assessment of population parameters has concentrated on populations of large migratory baleen whales (*e.g.*, Chaloupka *et al.* 1999; Mizroch *et al.* 2004; Ramp *et al.* 2006, 2010) or cetaceans that inhabit coastal areas (*e.g.*, Verborgh *et al.* 2009). For the same reason, much of the available information has low precision, which leads to low power to detect trends in the stocks (see Taylor *et al.* 2007).

Coastal dolphin populations have been the subject of some of these studies (*e.g.*, Cameron *et al.* 1999, Parra *et al.* 2006, Lukoschek and Chilvers 2008, Reisinger and Karczmarski 2010). However, even for the well-studied cosmopolitan bottlenose dolphin (*Tursiops* spp.), we lack vital information for most populations. For instance, few

studies have reported population-specific survival rates (but see Currey *et al.* 2009). Recently, however, such estimation procedures have been improved by including the effects of transience and temporary emigration (Silva *et al.* 2009).

Guiana dolphins (*Sotalia guianensis*) occur exclusively in shallow and coastal waters of the western Atlantic Ocean (15°N to 27°S, Silva and Best 1996). Recent studies have primarily addressed general biology (*e.g.*, Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Wedekin *et al.* 2007) and behavior (*e.g.*, Daura-Jorge *et al.* 2005, Filla and Monteiro-Filho 2009). There are few instantaneous estimates of Guiana dolphin abundance or density, and both survival rates and population trends are unknown. This central theme in ecology highlights one of the main gaps in the body of knowledge about this species. Moreover, as anthropogenic disturbances increase, population dynamics receives increased emphasis, as it supplies appropriate analytical tools for conservation purposes.

Guiana dolphin populations are frequently exposed to human activities because they inhabit coastal areas (Borobia *et al.* 1991). Mortality due to accidental (*e.g.*, Di Benedetto 2003) and intentional catches (Sholl *et al.* 2008), boat strikes (*e.g.*, Van Bressen *et al.* 2007), behavioral disturbances due to boat traffic (*e.g.*, Araújo *et al.* 2008), skin diseases (*e.g.*, Van Bressen *et al.* 2009), and high levels of persistent contaminants in tissues (*e.g.*, Yogui *et al.* 2003) are known threats to this species. Effective monitoring efforts that provide robust estimates of a set of population parameters are therefore a necessity. More importantly, these studies will fill the data and knowledge gaps that currently preclude a definition of conservation status for this species (*Data deficient*, Reeves *et al.* 2008).

We conducted a long-term mark-recapture experiment on the eastern Brazilian coast to study the population dynamics of Guiana dolphins. Our main objective was to estimate key population parameters such as survival and abundance of a population composed of resident and transient individuals in a heterogeneous habitat. To investigate possible changes in population size, a further aim of this study was to assess our likelihood of detecting a population decline.

MATERIALS AND METHODS

Study Area

This study encompassed the Caravelas River estuary (17°30'S, 39°30'W) and adjacent coastal areas, spanning more than 700 km². It is located on the Abrolhos Bank, an extension of the continental shelf on the eastern coast of Brazil (Fig. 1). The region is highly heterogeneous, characterized by a mosaic of open waters protected by coral reef barriers, mangrove forests with channels, sandy beaches, and banks of shallow waters.

Data Collection and Sampling Design

A mark-recapture experiment was conducted using individual recognition through photo identification. For each animal a capture history was created, where a capture event in a sampling occasion was denoted as 1 (here a photographic record) and a not capture as 0. From maximum likelihood estimation procedures, we derived the population parameters that maximize the likelihood of observed our capture histories frequencies (Lebreton *et al.* 1992).

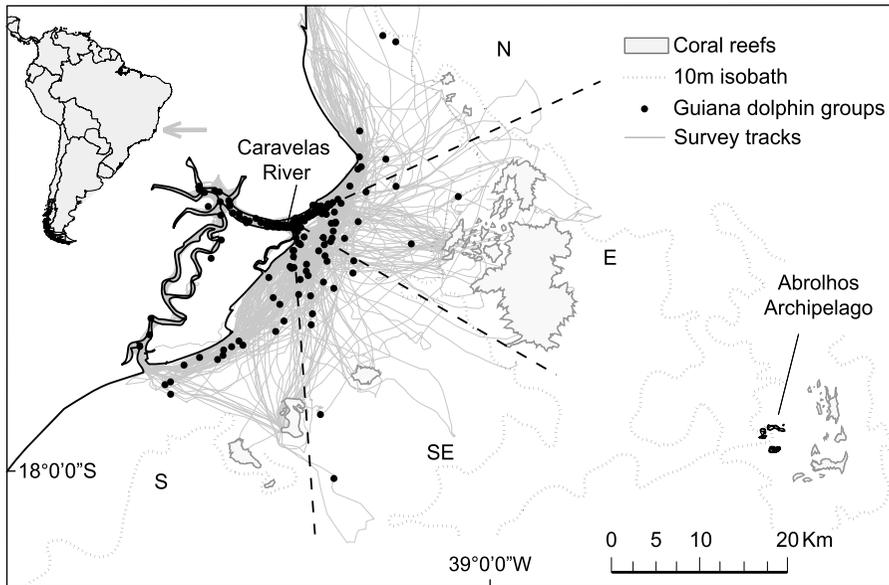


Figure 1. Caravelas River Estuary, coastal adjacent waters and coral reefs in the Abrolhos Bank, eastern coast of Brazil. Black dots indicate groups with identified Guiana dolphins.

Data collection was carried out during surveys using a 5 m inflatable boat (50 hp outboard engine) between 2002 and 2005, and using a 12 m wooden vessel (33 hp inboard engine) from 2006 to 2009. Routes aimed to cover the study area homogeneously: each covered an average of 30 nmi (56.6 km), including departing and arriving at the estuary, and aimed to sequentially sample four different subregions within the study area (north, east, southeast, and south; Fig. 1). Given the period required to cover the whole area, four consecutive sampling days were pooled and treated as a capture occasion.

Groups of dolphins were searched at slow speed (up to 5 kn) by two to five observers, alternating in three positions to cover 180 degrees of the visual field. For all sightings, we recorded geographic coordinates, time, and the number of individuals. We attempted to photograph the dorsal fin of all dolphins in the group, taking as many photos as possible of both sides and without individual preferences. Because individuals cannot be recognized during the data collection, the capture effort was assumed equal for all animals. From April 2002 to July 2004, photographs were taken using a SLR camera (Nikon N-90), equipped with 300, 70–300, and 120–400 mm lenses. In August 2004 we switched to digital SLR cameras (Nikon D70 and more recently D80) and the same lenses.

Photo-Identification

Guiana dolphins were identified by natural markings on the dorsal fin, a technique widely used for individual recognition of cetacean species (Hammond *et al.* 1990), including Guiana dolphins (*e.g.*, Flores 1999). During 2002 and 2004, the slide films were projected onto a white surface to produce profile drawings of each marked

dorsal fin (adapted from Defran *et al.* 1990; see Rossi-Santos *et al.* 2007). The digital catalog with photos from the entire period was periodically reviewed and included only high quality photographs (good focus and perpendicular angle). To minimize misidentification, the photo analysis was restricted to individuals with a very distinctive dorsal fin (at least one long-lasting notch on the trailing edge, Hammond *et al.* 1990). Calves and nonidentifiable individuals (intact or indistinctive dorsal fin, or captured only on low-quality photographs) were not included in our analyses.

Discovery Curves

To visualize differences in sampling effort among years and to provide a valid comparison of the number of identified individuals under varying sampling effort, discovery curves were generated using the same method as for sample-based rarefaction curves (Gotelli and Colwell 2001). These are more robust surrogates of the traditional cumulative curves, representing the means of repeated resampling of the capture occasions at random and plotting the average number of marked individuals (Gotelli and Colwell 2001). Resampling was done by Monte Carlo methods, setting 1,000 iterations and the expected curves were developed as a function of number of samples (Mao Tau) in the software EstimateS (Colwell RK, <http://purl.oclc.org/estimates>).

Mark-Recapture Analysis

Mark-recapture analyses were conducted using Program MARK (White and Burnham 1999). We used Cormack–Jolly–Seber (CJS) models for open populations (Cormack 1964, Jolly 1965, Seber 1965) to estimate apparent survival (ϕ) and capture probability (p). Departing from the full time varying CJS model, a set of candidate models were developed to test different effects on the estimated parameters: no variation (\cdot), time dependence (t); time since marking, *i.e.*, age-dependence ($a2$); and the set of dolphins identified in a given occasion (*cohort*) (Lebreton *et al.* 1992). Because sampling effort varied during the study, we also introduced a *period* effect in the models, representing the variation of effort among the first 3 yr and the last 4 yr. The first 3 yr were characterized by broader sampling efforts with analog cameras, whereas in the later years, effort was reduced and digital cameras were used.

Mark-recapture models make the following assumptions (see Amstrup *et al.* 2005): (1) marks are not lost during the study, (2) marks are correctly recognized on recapture, (3) individuals are instantly released after being marked, (4) intervals between sampling occasions are longer than the duration of the sample, (5) all individuals observed during a given sampling occasion have the same probability of surviving to the next one, (6) study area does not vary, and (7) marked and unmarked animals have equal capturability. We relied on the validation of open population assumptions for dolphins discussed by Silva *et al.* (2009). In addition, we validated the assumptions of equal probabilities of capture and survival by the goodness-of-fit test using program RELEASE (Lebreton *et al.* 1992). Even if one or more assumptions failed, the occurrence and magnitude of the resulting extra-binomial variation (*overdispersion*, see Anderson *et al.* 1994) was evaluated and accounted for. We estimated the variance inflation factor (\hat{c}) through the Median \hat{c} and bootstrap approaches, available in Program MARK (White and Burnham 1999), and used the highest value to adjust the lack of fit of the models.

Pollock's Robust Design (RD) (Pollock 1982; Kendall *et al.* 1995, 1997) was applied to assess population size and emigration pattern. A year was considered as the primary period and used to estimate apparent survival. The 4 d pooled capture occasions within each year were set as the secondary periods and used to estimate abundance through closed-population models. The modifications on RD by Kendall *et al.* (1997), which allow for an animal in the population to be unavailable for capture at a given time, were used to estimate temporary emigration.

The models based on the RD were composed of the following parameters: ϕ_t = the apparent survival probability from primary period t to $(t + 1)$; p_{st}, c_{st} = the probability that an individual available for capture in period t would be recaptured in the secondary sample s of the primary period t ; $\gamma'_t \gamma''_t$ = the probability that an individual would be unavailable for capture during primary period t given that it was unavailable or available (respectively) in the previous period (*i.e.*, the probability of temporary emigration). Population size (\hat{N}) was estimated using the full parameterization of maximum likelihood available in MARK (White and Burnham 1999). The following models were designed using the notation provided by Kendall *et al.* (1997): Markovian emigration models ($\gamma' \gamma''$), where the probability of availability depends on whether the animal was available for capture; random emigration models ($\gamma' = \gamma''$), where the probability of availability is completely random; and models with no emigration ($\gamma' = \gamma'' = 0$).

The eight classical closed population models (Otis *et al.* 1978) used in the RD (Kendall *et al.* 1995) have other specific assumptions for the secondary period (for assessment of assumptions to cetacean data, see Wilson *et al.* 1999, Bearzi *et al.* 2008): (1) demographic closure; (2) lack of behavioral responses to capture procedure, *i.e.*, animals do not respond to being captured in a way that affects their subsequent probability of recapture; and (3) homogeneity of capture probabilities, *i.e.*, within a sampling occasion, all animals in the population have equal probability of being captured. Behavioral response models were discarded because we assumed *a priori* there were no reactions to the capture procedure involving photo-identification (*trap dependence*). Thus, the capture probability (p) was considered equal to the recapture probability (c). Individual heterogeneity was included using the Pledger's mixture models, with two mixtures of capture probabilities ($2 - \pi$) (Pledger 2000). However, heterogeneity in capture probabilities was included only in those models with no emigration. The influence of time was tested for all parameters, both in primary periods (t) and secondary periods (s).

For the CJS approach, the most appropriate model was selected through the Quasi-Akaike Information Criterion (QAIC_c, Anderson *et al.* 1994), while the Akaike Information Criterion (AIC_c) was used for RD models. In all cases, specific biological hypotheses between nested models were tested using likelihood ratio tests (LRT, Burnham and Anderson 2002). Normalized QAIC_c weights—or AIC_c weights for RD models—were used to measure the support for a given model relative to the others. Parameter estimates were averaged across all models based on QAIC_c—or AIC_c—weights (Burnham and Anderson 2002).

Trends in Abundance

Because the abundance estimates (\hat{N}) refer exclusively to the well-marked animals in the population, we corrected this to include the unmarked individuals in the total abundance estimates (\hat{N}_θ). For each year, the proportion of identifiable individuals within the population (θ) was estimated as the number of well marked individuals

Table 1. Summary of annual sampling effort and basic results of the long-term mark-recapture experiment with Guiana dolphins (*S. guianensis*) carried out in the Caravelas River estuary, eastern Brazil.

Year	Sampling effort		Total observation (h)	4 d capture occasions	Sighted groups	Mean group size \pm SD	Total sighted dolphins (calves)
	(nmi)	(h)					
2002	2,340.6	327.0	60.7	11	72	4.2 \pm 2.1	316 (39)
2003	2,784.4	465.3	58.3	19	78	5.2 \pm 3.1	385 (34)
2004	2,214.1	280.7	27.5	14	53	4.0 \pm 1.8	201 (13)
2005	1,529.4	258.8	44.9	12	40	5.6 \pm 4.1	217 (29)
2006	668.6	122.1	22.1	6	22	4.2 \pm 1.2	100 (15)
2007	1,035.7	217.6	16.7	8	37	5.4 \pm 2.8	165 (17)
2008	1,518.3	297.8	21.7	11	46	4.5 \pm 2.5	177 (15)
2009	1,333.4	266.0	16.1	11	32	4.6 \pm 2.2	141 (8)

divided by the total number of individuals observed in each group, averaged over all groups (*cf.* Silva *et al.* 2009). Other similar methods for theta estimation are available (*e.g.*, Williams *et al.* 1993), but particularities of this population make our approach feasible. Because Guiana dolphins usually form small groups in the Caravelas River estuary (Table 1), and generally a single group was sighted in each day ($\bar{x} = 1.26 \pm 0.33$ SD), the number of marked individuals in each group could be estimated with precision.

The total abundance estimates were obtained by

$$\hat{N}_\theta = \frac{\hat{N}}{\theta},$$

and the variances of total population size were estimated using the delta method (Seber 1982) as:

$$\text{var}(\hat{N}_\theta) = \hat{N}_\theta^2 \left(\frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{1 - \theta}{n\theta} \right),$$

where n is the total number of individuals from which \hat{N} was estimated. Log-normal confidence intervals for total population size (see Burnham *et al.* 1987) were calculated as:

$$C = \exp \left[z_{\frac{\alpha}{2}} \times \sqrt{\ln \left(1 + [\text{CV}(\hat{N}_\theta)]^2 \right)} \right],$$

where z is the normal deviate, $\alpha = 0.05$, and CV is the coefficient of variation.

To determine the probability of detecting a linear population trend in the corrected abundance estimates, we performed a statistical power analysis (Fairweather 1991). By definition, a trend exists when the regression has a slope significantly different from zero (see Gerrodette 1987). Power analysis provides the probability of correctly rejecting the null hypothesis of constant population when it is actually increasing or decreasing ($1 - \beta$, where β is the probability of Type 2 error).

To explore the monitoring efficiency, we simulated two kinds of changes in the population: a precipitous decline of 50% in the abundance during the entire monitoring period (*e.g.*, Taylor *et al.* 2007) and a modest decline of 5% per year (*e.g.*, Lukoschek and Chilvers 2008). We analyzed the effort necessary to detect these changes with an acceptable power of 80% certainty (see Taylor *et al.* 2007).

Analyses were conducted using the software TRENDS (Gerrodette 1987, 1993), setting the parameters as follows: the significance criterion $\alpha = 0.05$; one-tailed test (because we are only concerned with a decrease); equal intervals between sampling occasions and exponential type of change. Corrected abundance estimates (\hat{N}_t) were transformed to the natural logarithm before performing the regression. Variance usually fluctuates according to some function of the abundance (Gerrodette 1993), and for mark-recapture estimates, the CV on abundance is expected to be proportional to the square root of abundance (Gerrodette 1987). However, it can also vary due to the species and the method used. To test this, we plotted CVs of each year against $\sqrt{\hat{N}_t}$ and $(\sqrt{\hat{N}_t})^{-1}$ (*cf.* Gerrodette 1987). Since no clear relationship arose, we assumed CVs were constant with respect to abundance and thus calculated the overall CV of the monitoring period by averaging the annual CVs (Gerrodette 1993).

RESULTS

Sampling Effort

From 2002 to 2009, sampling was performed on 389 d and covered more than 13,425 nmi. We recorded 380 groups, totaling 1,702 sighted dolphins (10% calves) (Table 1). A total of 108 individuals were identified with good-quality photographs, and 12 were resighted in all years. Greater sampling effort was employed between 2002 and 2004 than in the later years. The number of individuals with long-lasting marks included in the analysis varied among years (Table 1). The rarefaction curves for 2002 to 2004 tended to stabilize with narrower confidence intervals (Fig. 2A, B). The opposite was found for surveys from 2005 on, when all confidence intervals were wider, and the curves were nonasymptotic (Fig. 2B–D). The number of new photo identified individuals per year fluctuated from 15 (2004) to 40 (2007), while the recapture rate varied from 55% (2007) to 86% (2004). From 30% to 64% of photo-identified dolphins in one year were recaptured in the subsequent year (Table 2).

Model Selection for Estimating Population Parameters

From the results of all components of the goodness-of-fit test, we did not violate the assumptions of equal probabilities of capture (TEST 2; $P = 0.778$) and survival (TEST 3; $P = 0.522$). The most parameterized CJS model fitted our data satisfactorily. The bootstrap approach estimated the highest variation inflation factor, which was marginally above 1 and indicated no substantial overdispersion ($\hat{c} = 1.25$). It may be caused by the presence of temporary emigrants in the population, or other source of heterogeneity of capture probability (see further). Despite the lack of evidence for such an effect, we adjusted the models with \hat{c} to correct any potential violation of assumptions or intrinsic variations in the population.

In general, the CJS models with time (Table 3: models 15, 13, 12) or age-dependence (models 6, 3) of survival and models that allowed this parameter to vary with sampling effort (models 14, 9, 5) poorly fit the data or were not parsimonious.

Table 3. Cormack–Jolly–Seber models for survival (φ) and capture probability (p) ranked by the lowest QAIC_c. QAIC_c weight indicates the strength of evidence for a given model. Model notation: constant parameter (\cdot), time (t), age ($a2$), *cohort* or *period* dependence.

Model	QAIC _c	Δ QAIC _c	QAIC _c weights	Likelihood	No. parameters
1 $\{\varphi(\cdot) p(\text{cohort})\}$	411.621	0	0.468	1	8
2 $\{\varphi(\cdot) p(\text{cohort} \times \text{period})\}$	413.487	1.87	0.184	0.393	10
3 $\{\varphi(a2) p(t)\}$	413.487	1.87	0.184	0.393	9
4 $\{\varphi(\cdot) p(t)\}$	415.639	4.02	0.063	0.134	8
5 $\{\varphi(\text{period}) p(t)\}$	417.302	5.68	0.027	0.058	9
6 $\{\varphi(a2) p(\cdot)\}$	417.414	5.79	0.026	0.055	3
7 $\{\varphi(\cdot) p(t + \text{period})\}$	417.825	6.21	0.021	0.045	9
8 $\{\varphi(\cdot) p(\cdot)\}$	419.019	7.40	0.012	0.025	2
9 $\{\varphi(\text{period}) p(\cdot)\}$	420.802	9.18	0.005	0.010	3
10 $\{\varphi(\cdot) p(\text{period})\}$	420.929	9.31	0.005	0.010	3
11 $\{\varphi(\cdot) p(t \times \text{period})\}$	422.266	10.64	0.002	0.005	11
12 $\{\varphi(t) p(t)\}$	423.331	11.71	0.001	0.003	14
13 $\{\varphi(t) p(\cdot)\}$	423.561	11.94	0.001	0.003	8
14 $\{\varphi(\text{period}) p(t \times \text{period})\}$	423.996	12.38	0.001	0.002	12
15 $\{\varphi(t) p(\text{period})\}$	425.732	14.11	0	0.001	9
16 $\{\varphi(\cdot) p(\text{cohort} \times t)\}$	439.523	27.90	0	0	29

Model (model 1). In general, those models in which survival was time-dependent (models 6–8 and 10–12) and which allowed capture probability to vary between secondary periods (model 12) were not parsimonious or poorly fit the data. Thus, the best RD model had random and constant emigration probabilities, constant survival and time-dependent capture probability between and within primary periods (model 1). When comparing nested models, the LRT corroborated a constant survival (model 4, $P = 0.205$) and random emigration pattern (model 2, $P = 0.165$), but it suggested a temporal effect on the probability of an individual being unavailable for capture (γ ; model 3, $P = 0.012$).

Survival and Capture Probability

Apparent survival rates were high and stable during the study. The model-averaged estimates of both approaches provided similar results: CJS: $\varphi = 0.88 \pm 0.07$ SE, 95% CI = 0.67–0.96; RD: $\varphi = 0.89 \pm 0.03$ SE, 95% CI = 0.82–0.94.

CJS models detected fluctuations in recapture probabilities between cohorts throughout the monitoring (Fig. 3). Capturability was lower for the 2004 cohort ($p = 0.215 \pm 0.143$ SE) and reached maximum values in 2003* ($p = 0.629 \pm 0.124$) and 2009 ($p = 0.633 \pm 0.186$).

Emigration Probability

We used model-averaged results from the RD models to investigate individual movements. Specifically, we estimated the probability that an individual available

*Year corrected after online publish date of 1 March 2011.

Table 4. Pollock's Robust Design models for survival (φ), temporary emigration (γ), capture (p), and recapture probabilities (c) ranked by the lowest AIC_c . AIC_c weight indicates the strength of evidence for a given model. Model notation: no emigration ($\gamma'' = \gamma' = 0$); Markovian emigration ($\gamma'(x) \gamma''(x)$); random emigration ($\gamma'(x) = \gamma''(x)$); mixture proportion (π); no behavior effect ($p(x) = c(x)$); constant parameter (\cdot) or time-dependence (t, s).

Model	AIC_c	ΔAIC_c	AIC_c weights	Likelihood	No. parameters
1 $\{\varphi(\cdot) \gamma''(\cdot) = \gamma'(\cdot) p(st) = c(st)\}$	1,717.222	0	0.540	1.000	102
2 $\{\varphi(\cdot) \gamma''(\cdot) \gamma'(\cdot) p(st) = c(st)\}$	1,718.401	1.180	0.300	0.555	103
3 $\{\varphi(\cdot) \gamma''(t) = \gamma'(t) p(st) = c(st)\}$	1,719.735	2.510	0.154	0.285	108
4 $\{\varphi(t) \gamma''(\cdot) = \gamma'(\cdot) p(st) = c(st)\}$	1,727.640	10.420	0.003	0.006	108
5 $\{\varphi(\cdot) \gamma''(t) \gamma'(t) p(st) = c(st)\}$	1,728.688	11.470	0.002	0.003	114
6 $\{\varphi(t) \gamma''(\cdot) \gamma'(\cdot) p(st) = c(st)\}$	1,729.797	12.580	0.001	0.002	109
7 $\{\varphi(t) \gamma''(t) = \gamma'(t) p(st) = c(st)\}$	1,731.990	14.770	0.000	0.001	114
8 $\{\varphi(t) \gamma''(t) \gamma'(t) p(st) = c(st)\}$	1,744.131	26.910	0	0	120
9 $\{\varphi(\cdot) \gamma'' = \gamma' = 0 p(st) = c(st)\}$	1,764.346	47.120	0	0	101
10 $\{\varphi(t) \gamma'' = \gamma' = 0 \pi(\cdot) p(s)\}$	1,768.690	51.470	0	0	32
11 $\{\varphi(t) \gamma'' = \gamma' = 0 p(st) = c(st)\}$	1,772.300	55.080	0	0	107
12 $\{\varphi(t) \gamma'' = \gamma' = 0 p(s) = c(s)\}$	1,880.055	162.830	0	0	23

for capture on previous occasions temporarily emigrated from the study area (γ''), and the probability that an individual that was outside the study area on a previous occasion remained outside it (γ'). Under a Random Movement model, temporary individual emigration from the sampled area to neighboring regions was the same for a given emigrant remaining outside of the study area ($\gamma'' = \gamma' = 0.33 \pm 0.07$ SE; 95% CI = 0.20–0.49). Thus, the probability of dolphins remaining in the study area between capture occasions ($1 - \gamma''$) and the return rate of temporary emigrants to the study area were equal ($1 - \gamma'' = 1 - \gamma' = 0.67$). In addition, the probability that a given dolphin moved between the study area and the adjacent areas appeared not to depend on its location during the previous sampling occasion (see Kendall *et al.* 1997).

Abundance Estimates

The number of dolphins using the study area varied among years, though not significantly. The averaged RD model yielded annual abundance estimates ranging from 25 to 69 marked dolphins, which were corrected to a total of 57–124 individuals (Table 5). Even with apparent peaks in the years 2004 and 2009, abundance was apparently constant across the years (Fig. 4).

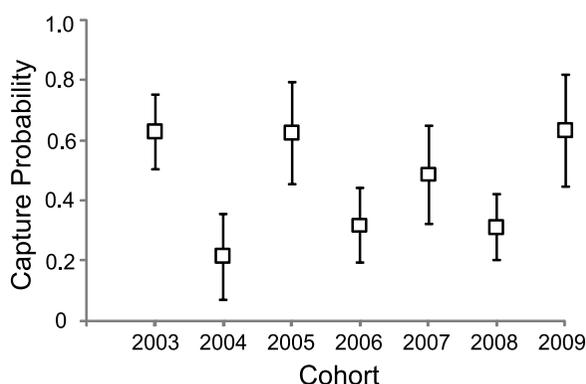


Figure 3. Capture probability estimates for the seven cohorts of Guiana dolphins in the Caravelas River estuary, based on the averaged Cormack–Jolly–Seber model. Whiskers represent standard error.

Table 5. Abundance estimates (\hat{N}) of the Guiana dolphin population in the Caravelas River estuary for each year from the averaged Robust Design model, with corrections (\hat{N}_θ) to include the unmarked individuals.

Year	Proportion of marked dolphins		RD abundance estimates					
	θ	SE (θ)	\hat{N}	CV	95%CI	\hat{N}_θ	CV	95%CI
2002	0.53	0.065	37	0.027	35–39	70	0.123	55–89
2003	0.39	0.055	31	0.031	29–33	79	0.143	60–105
2004	0.24	0.060	25	0.251	13–37	105	0.354	53–204
2005	0.54	0.059	37	0.061	32–41	67	0.117	55–86
2006	0.59	0.091	34	0.163	23–44	57	0.215	38–87
2007	0.55	0.062	55	0.128	41–69	100	0.169	72–139
2008	0.38	0.079	34	0.144	25–43	89	0.246	56–144
2009	0.56	0.078	69	0.153	48–90	124	0.201	83–182

Trends in Abundance

The regression of the corrected abundance estimates (\hat{N}_θ) throughout the monitoring period was not significant ($t = 1.372$, $P = 0.219$; Fig. 4). The precision of estimation was moderate (CV = 0.196; see Taylor *et al.* 2007), and the statistical power to detect the change indicated by the regression coefficient ($b = 0.051$) was reasonable ($1 - \beta = 0.43$).

The minimum rate of population decline detectable with acceptable statistical power ($1 - \beta = 0.8$) was an overall decrease of 45% or an annual decrease of 8%. Our monitoring showed sufficient power ($1 - \beta = 0.90$) to detect a precipitous decline of 50% in the population during the entire study. In order to detect a slight decrease of 5% per year ($1 - \beta = 0.45$), additional three years to our sampling effort to date would be required (11 yr of monitoring; Fig. 5).

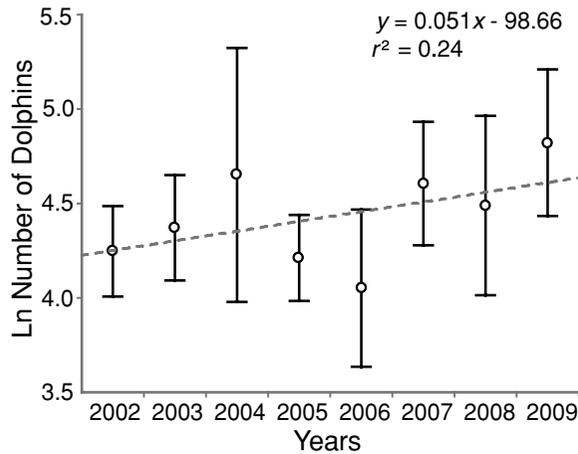


Figure 4. Regression line of ln-transformed annual abundance estimates (through averaged RD model and theta correction) of the Guiana dolphin population in the Caravelas River estuary. Whiskers represent 95% confidence intervals.

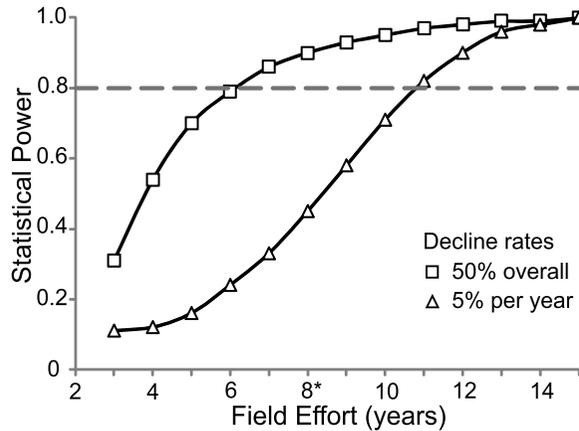


Figure 5. Statistical power to detect changes in the population of Guiana dolphins in the Caravelas River estuary under two different scenarios: a decline of 50% during the entire monitoring period and a decline of 5% per year. The horizontal dashed line represents a probability of 80% of detecting a change. Asterisk represents the current monitoring period.

DISCUSSION

There are three important outcomes of this study. From a local perspective, we have highlighted the importance of long-term monitoring in understanding the hitherto unknown population dynamics of Guiana dolphins within a highly heterogeneous habitat. From a regional view, the first estimates of several population parameters are provided for this species. Our work helps to fill the knowledge gaps that preclude definition of conservation status for Guiana dolphins, as anthropogenic disturbances threaten many populations. In a broader scale, our results confirm the feasibility of

monitoring frameworks based on robust mark-recapture modeling of free-ranging cetacean data.

Survival

The most parsimonious models considered a constant and high apparent survival probability throughout the study period. High adult survival is expected for large and slowly reproducing mammals, whose life span is longer than the study duration (e.g., Zeh *et al.* 2002). Although there is no other survival estimate available for Guiana dolphins, our survival rate is similar to that of bottlenose dolphins (*Tursiops truncatus*). Few studies have derived survival probabilities of small cetaceans from mark-recapture analyses (e.g., Cameron *et al.* 1999, Currey *et al.* 2009, Silva *et al.* 2009), but other methodologies (e.g., Wells and Scott 1990, Stolen and Barlow 2003) have also shown adults with relatively high survival probabilities.

Capturability

Capture probabilities fluctuated across cohorts, and indicated that individuals captured for the first time in each year showed different probabilities of being recaptured. This parameter is expected to be constant across cohorts only when recapture is similar among all individuals. Since it is a product of the probability of being detected and of being present in the sampled area (Lebreton *et al.* 1992), one may expect cohorts to differ due to differences in sampling effort and individual site fidelity.

We considered two potential explanations for variability in capture probabilities. First, differences in our monitoring scheme, especially the switch from analogical to digital photographic equipments, were expected to lead to variations in capturability. With less cost, more photographs were taken and laboratory tools for photo manipulation (e.g., zoom, contrast) became more accessible. Thus, capture efficiency may be enhanced using digital photo identification techniques (Markowitz *et al.* 2003). However, models incorporating such sampling variation in capture probability poorly fit our data and actually failed to explain such fluctuations.

Alternatively, capture probability may have been influenced by variations in residence patterns. Since transient dolphins have high probability of being unavailable for capture on subsequent occasions (Pradel *et al.* 1997), a higher proportion of these individuals in a given year will result in a lower capture probability. In our case, fluctuations in capture probability matched the number of photographed dolphins in each year, which in turn reflected the relative proportion of nonresident individuals sampled annually (see Silva *et al.* 2009). This situation is corroborated by the existence of dolphins passing through our study area (Rossi-Santos *et al.* 2007) and by the evidence of an annual variation in emigration probabilities (based on LRT results).

Emigration Patterns

Movements of animals can invalidate the assumption of homogeneous capture probabilities (Lebreton *et al.* 1992). Variation in site fidelity among individuals has been suggested for this species (e.g., Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004) and for our studied population as well. The latter is composed of a core of year-round, long-term resident individuals and many others that show low site fidelity to the Caravelas River estuary (Rossi-Santos *et al.* 2007). This evidence

indicates that dolphins temporarily emigrate from or immigrate to our study area. Therefore, by relying on RD general framework, it was possible to quantify such movements and presumably obtain unbiased estimates for other parameters (Pollock 1982, Kendall *et al.* 1997, Silva *et al.* 2009). Temporary emigration from the sampled area (33%) and return rates from neighboring regions (about 67%) were moderate during the monitoring period.

The incidence of temporary emigration combined with significant probabilities of remaining away from the area and varying site fidelity suggest that some individuals use other areas beyond the study area (see Fortuna 2006). Caravelas River estuary and vicinity comprise one of the largest studied areas for this species (more than 700 km²), and at the same time the area presents a patchy mosaic of habitats, encompassing closed and open waters. This pattern is different from other localities where the species has been studied: usually small areas where most sampling effort was restricted to protected bays (Flores 1999, Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Cremer 2007, Wedekin *et al.* 2007, Flach *et al.* 2008, Filla and Monteiro-Filho 2009). Guiana dolphins have been sighted in all regions adjacent to our study areas (Rossi-Santos *et al.* 2006), and habitats commonly used by the species in the Abrolhos Bank include estuarine systems, open coastal areas, shallow reef banks, and offshore islands (Rossi-Santos *et al.* 2006). It is reasonable to suppose that individual stratification of habitat use exists (see Wilson *et al.* 1997), given the small home ranges recorded for the species (Flores and Bazzalo 2004, Rossi-Santos *et al.* 2007, Wedekin *et al.* 2007) and the heterogeneity of habitats commonly used by the dolphins in the Abrolhos Bank.

Population Size

Population size fluctuated during the monitoring, possibly because of interannual variation in the balance between additions (births or immigration) and deletions (deaths or emigration) in the population. For example, abundance reached its lowest level in 2006, but was much higher in 2004 and 2009. Such fluctuations in abundance, combined with the ranging patterns and residence levels, suggest the existence of a *super-population* (*sensu* Schwarz and Arnason 1996) using the study area (see Kendall 1999). The dolphins sighted at the beginning of the monitoring period were not the same individuals seen in later years. Some were resighted during the study, but many others may have left the area or the population.

Nevertheless, the Caravelas River estuary holds a relatively small population of Guiana dolphins. As abundance estimates are only available for a few other populations, then opportunities for comparison are limited. Most of these estimates were obtained through strip or line transects sampling (Buckland *et al.* 2001). Few studies conducted mark-recapture analysis, and only through classical closed population models (see Chao and Huggins 2005 for a review). These models might include an unknown degree of bias (see Hammond 1990). Putting this possibility aside, it seems that most populations were estimated to consist of <100 (Pizzorno 1999, Edward and Schnell 2001) or a few hundred individuals (Geise 1991, Geise *et al.* 1999, Acuña 2002, Cremer 2007). One large population of more than a thousand dolphins was studied in southeastern Brazil (Flach *et al.* 2008), but this is probably an exception for the species.

Population Trends

Trends in abundance offer a clear indication of the health of a population (Williams *et al.* 2002). Assessment of such temporal changes is a priority recommendation for the

species, from both local and global perspectives (IBAMA 2001, Reeves *et al.* 2008). The previous estimates of Guiana dolphin abundance provided only instantaneous information. This is the first study to provide a time-series of abundance estimates and is the first attempt to model population trends for the Guiana dolphin.

Despite annual fluctuations in abundance, the number of dolphins in the population of the Caravelas River estuary was apparently stable. We could not reject the null hypothesis of constant population size suggested by the regression coefficient of the ln-transformed annual point estimates. Monitoring low rates of population change of highly mobile species in dynamic environments is truly difficult because such changes may be confounded with natural variability in abundance (Gerrodette 1987, Forney 2000). Our current effort is not yet sensitive to slight variations in population size. However, sufficient time to identify such variations is feasible (estimated to be 11 yr of monitoring). This fact reinforces that long-term efforts are required to ensure reliability of conclusions about changes in population size.

The power to detect upward or downward trends is directly related to the precision of abundance estimates as well as to the rate of change in population size and to the monitoring duration (Gerrodette 1987, Fairweather 1991, Wilson *et al.* 1999, Taylor *et al.* 2007). Our study represents a case of relatively precise abundance estimates (see Taylor *et al.* 2007) and the monitoring scheme we have applied would be able to detect abrupt abundance changes with high certainty. This situation is much better than most other cetacean species. For example, the power to detect a precipitous decline (50% in 15 yr) in this Guiana dolphin population ($1 - \beta = 1.00$) is much higher than for the majority of studied stocks: over the same sampling period, power is between 0.00 and 0.50 for more than 85% of large whales and more than 95% of delphinid stocks (see fig. 1 in Taylor *et al.* 2007).

Even with an apparently stable population of Guiana dolphins in the Caravelas River estuary, the species is exposed to several long-term human-related threats in the area and throughout its distribution. Typically, many simultaneous threats affect populations' local persistence (Wedekin *et al.* 2005, Filla *et al.* 2008). While the cumulative effect of these impacts is not fully evident, a cautious and conservative interpretation should be maintained, especially because the species is a habitat specialist and small populations are scattered along the coast. Sustained monitoring effort is therefore required for effective management of this species and its habitats.

Conclusions

This study represents a first step towards understanding the population dynamics of Guiana dolphins. Our results shed light on the importance of long-term monitoring of the species, especially considering that anthropogenic pressures are expected to increase in coastal habitats in the future. A robust baseline for conducting population monitoring was based on open and closed population mark-recapture models applied to photo-identification data. Reliable parameter estimates from other Guiana dolphin populations are urgently needed to allow further comparisons and to yield an adequate evaluation of the conservation status of the species.

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