



Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil

FÁBIO G. DAURA-JORGE,¹ Pós-Graduação em Ciências Biológicas, Zoologia, Universidade Federal do Paraná, PO Box 19020, CEP 81531–980, Curitiba, Paraná, Brazil; SIMON N. INGRAM, The Marine Institute, Plymouth University, Plymouth PL4 8AA, United Kingdom; PAULO C. SIMÕES-LOPES, Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, PO Box 5102, 88040–970, Florianópolis, Santa Catarina, Brazil.

ABSTRACT

A subgroup of a population of *Tursiops truncatus* in southern Brazil is known for a cooperative behavior with artisanal fishermen whereby the dolphins shoal fish towards net-casting fishermen. Combining photo-identification data collected between September 2007 and 2009 with mark-recapture and Pollock's robust design models, we assessed abundance within seasons and survival and temporary emigration rates of dolphins between seasons. We also reanalyzed a previous data set collected during 1989–1991, and Cormack-Jolly-Seber models were applied to estimate survival rates for each of the study periods. The abundance of marked “cooperative” dolphins varied between seasons from 18 (CI: 17–24) to 21 (CI: 20–24). The total abundance varied from 59 in the winter of 2008 (CI: 49–72) to 50 in the autumn of 2009 (CI: 40–62). The annual adult survival was estimated to be 0.917 (CI: 0.876–0.961), close to that estimated from data collected in the 1990s (0.941; CI: 0.888–0.998). The emigration probability was low (0.031; CI: 0.011–0.084) and different capture probabilities between the “cooperative” and “noncooperative” dolphins indicated a degree of behavioral segregation. The precision of our estimates is likely to provide sufficient power to detect population change, but we recommend a precautionary management approach to protect this vulnerable dolphin community and its unique cooperative feeding tradition.

Key words: population parameters, mark-recapture models, abundance, survival rates, temporary emigration, *Tursiops truncatus*, robust design.

Bottlenose dolphins (*Tursiops truncatus*) are distributed throughout tropical and temperate seas (Connor *et al.* 2000, Reynolds *et al.* 2000) and the species is well adapted to coastal habitats, frequently found in small and potentially isolated populations (*e.g.*, Wilson *et al.* 1999, Currey *et al.* 2007, Urian *et al.* 2009, Fruet

¹ Corresponding author (e-mail: daurajorge@gmail.com).

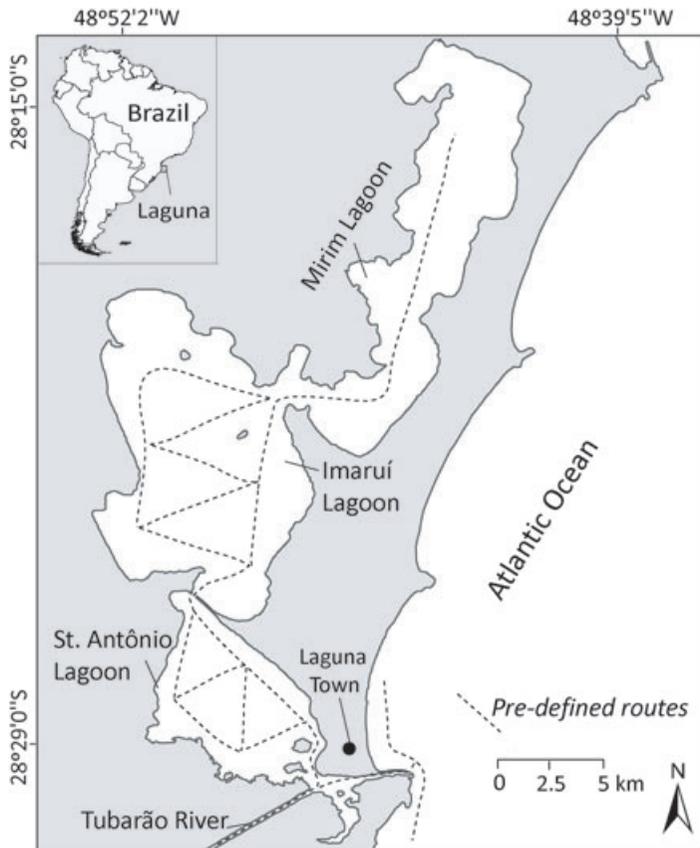


Figure 1. Location of the St. Antônio lagoon, the Imaruí lagoon, and the Mirim lagoon in southern Brazil. The dotted line represents the predefined sampling routes.

et al. 2011). A number of studies have described unique, localized foraging strategies in coastal populations of bottlenose dolphins around the world (*e.g.*, Hoese 1971, Simões-Lopes 1991, Chilvers and Corkeron 2001) that appear to be maintained by intergenerational social learning (Simões-Lopes *et al.* 1998, Krützen *et al.* 2005). The survival of these localized cultural behaviors depends on the maintenance of population health and habitat quality since it is extremely unlikely that these strategies will persist or be relearned if these traditional behaviors at specific coastal sites are interrupted or lost.

Bottlenose dolphins are often observed throughout the coastal waters of southern Brazil (Wedekin *et al.* 2008), but are concentrated in a few coastally resident communities such as the one found in the lagoon system near the town of Laguna (Fig. 1; Simões-Lopes and Fabian 1999). A number of dolphins belonging to this population are known for a unique fishing interaction with local artisanal fishermen (Pryor *et al.* 1990). The behavior seems to be a mutualistic cooperation and, despite occurring throughout the year, it is most frequently observed during the mullet season

(*Mugil* sp.) from austral autumn to early winter. The cooperation appears to be strongly ritualized; dolphins drive mullet schools towards a dynamic barrier of fishermen and “signal” with stereotyped behaviors, the right moment and where fishermen should throw their nets (see Pryor *et al.* 1990 or Simões-Lopes *et al.* 1998 for a detailed description).

The main aim of this study was to estimate the abundance, survival, and temporary emigration rates of dolphins using the coastal lagoon system at Laguna and to examine the numbers of animals within this population actively engaging in the cooperative fishing behavior. Only by measuring these parameters will the vulnerability of this population and the foraging tradition be more properly understood and protected. In 1999 the population was estimated at 51 individuals and appears to be strongly resident in the area (Simões-Lopes and Fabian 1999). Despite the occasional occurrence of transient individuals along the adjacent coast, photo-identification data indicate that nonmembers of this dolphin community are rarely observed within the lagoon system. However, at least two animals known from Laguna have been reported in Tramandaí, about 220 km to the south, where an adjacent community of bottlenose dolphins are resident (Simões-Lopes and Fabian 1999). Interestingly, the cooperative behavior with artisanal fishermen is also displayed at Tramandaí, indicating social learning and horizontal behavior transmission between adjacent communities (Simões-Lopes *et al.* 1998). These movements of individuals coincided with the mullet migratory season and involved individuals from Tramandaí or other adjacent areas, migrating into Laguna, at least temporarily, and *vice versa* (Simões-Lopes and Fabian 1999).

Mark-recapture analysis of photographic identification data is an effective and widely used approach to assess population parameters of various marine mammal species (*e.g.*, Bradford *et al.* 2008, Taylor *et al.* 2008, Silva *et al.* 2009, Verborgh *et al.* 2009, Mansur *et al.* 2011, Cantor *et al.* 2012). However, the movement of transient or nonresident individuals into and out of a study site may bias estimates of survival (Pradel *et al.* 1997) and abundance (Clavel *et al.* 2008). Therefore, despite the high site fidelity of dolphins in Laguna, this partial, seasonal migration must be considered in any estimate of the population size and survival of bottlenose dolphins belonging to the population in Laguna.

We selected Pollock’s robust design (RD) and modeled estimates of population size, apparent survival probabilities, temporary emigration rates, and capture probabilities, as well as evaluating the effect of factors such as time-dependence and particularly the cooperative behavior with fishermen on all these parameters. We also applied Cormack-Jolly-Seber open population models (CJS) to compare the survival probabilities of individuals during two study periods: (1) the current study (data collected during 2007–2009) and (2) a previous study (data collected during 1989–1991; Simões-Lopes and Fabian 1999). Finally, we evaluated our monitoring effort to assess the amount of time needed to detect significant population trends.

METHODS

Study Area

The coastal lagoon system adjacent to the town of Laguna (28°20’S–48°50’W) is comprised of three lagoons, the Mirim, Imaruí, and St. Antônio lagoons, which cover an area of approximately 300 km² (Fig. 1), and is one of largest such systems

in southern Brazil. The southern portion, the St. Antônio Lagoon, is fed by the Tubarão River and the other two lagoons, and connects to the Atlantic Ocean. In general, the lagoons are shallow, with an average depth of approximately 2 m, with the exception of the deep channel connecting the lagoon system to the ocean. The lagoon system is tidally dynamic and strongly influenced by prevailing winds (SE and NE) and rainfall (Meurer and Netto 2007). Where not urbanized or modified, the lagoon margins consist of wetlands and freshwater marshes, or small beaches and rocky shores. Currently no studies have described the water or sediment quality of the local habitat.

Data Collection and Sampling Design

From September 2007 to September 2009 we conducted photo-identification boat surveys to catalog the presence and locations of recognizable dolphins (Hammond *et al.* 1990). Field effort was planned to allow the use of robust design (RD; Pollock 1982, Kendall *et al.* 1997) and Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965, Lebreton *et al.* 1992) models. Each calendar season was considered a primary capture period and within each primary period, six capture surveys (photo-identification surveys) were conducted on separate days. One day was considered one sampling occasion so that each primary period (season) was comprised of six secondary periods (sampling days), totaling 48 field days (occasions). For CJS models the capture histories from the secondary periods (sampling days) were pooled into the four calendar seasons with each season treated as a single capture occasion.

A small (5 m) boat with a 15 hp engine was used to survey a 30 km predefined route and sample the area evenly during approximately 5 h of effort. We only included capture data from full surveys in which the predefined route was completed. A school of dolphins was defined as all individuals encountered within a 50 m radius of each other (Lusseau *et al.* 2003). When a school was encountered, the start time and location were recorded and attempts were made to photograph all the dolphins in the encounter, obtaining at least four pictures for each animal, preferably from both sides, and without individual preference (Würsig and Jefferson 1990). In order to minimize misidentification errors, individual identification was based on long-lasting natural marks on the dorsal fin (*e.g.*, Würsig and Jefferson 1990, Williams *et al.* 1993). In addition we only included good quality photographs (from a grading of poor, moderate, and good quality) and capture occasions with good weather conditions (Beaufort scale ≤ 3) in our analysis. Surveys on consecutive days were excluded to ensure the independence of capture events (Wilson *et al.* 1999).

Dolphins were classified as adults, subadults, and calves, according to size and color (following Cockcroft and Ross 1990). Calves were excluded from all analyses due to poor marking and because their movements are not independent of their mothers. Based on our field observations, dolphins were also classified according to their foraging strategy. Dolphins observed engaging in cooperative behavior—driving prey schools towards fishermen and performing stereotyped behaviors associated with the interaction (as described in Simões-Lopes *et al.* 1998)—were classified as cooperative dolphins. Dolphins that never drove prey schools or were never observed performing the stereotyped behaviors were classified as noncooperative dolphins.

CJS Modeling Procedures

The CJS models were applied to estimate apparent survival probability (Φ) between seasons and capture probabilities (p) for individuals in each season (Lebreton *et al.* 1992). We used this approach to compare survival estimates of individuals between primary sampling periods during the present study with estimates from data collected during the previous study between 1989 and 1991 (from Simões-Lopes and Fabian 1999). It should be noted that the survey effort during 1989–1991 used a different sampling design whereby the photo-identification procedure was conducted during three days per month from the shore, along the channel connecting the lagoon system to the ocean. Although this channel represents a core area where all identified dolphins were observed at least once a month (Daura-Jorge 2011), these data are potentially biased by heterogeneity in capture probability due to differences in the ranging behavior of individuals throughout the study site. Although we pooled data within each season to reduce this bias, comparisons between the two studies should be interpreted with caution.

We built a set of models to test time-dependent effects (t) and the effect of the foraging cooperation (g) (group membership defined by cooperative and noncooperative dolphins) on the estimated parameters. Considering the annual survival probability (Φ_a) as a cumulative result of the seasonal survival probabilities (Φ), we derived (Φ_a) from (Φ^4), and the coefficient of variation (CV) was estimated by:

$$CV(\Phi_a) = \sqrt{4 [CV(\Phi)^2]} \quad (1)$$

The log-normal confidence intervals were calculated following Burnham *et al.* (1987) (see Eq. 3).

RD Modeling Procedures

Pollocks robust design (Pollock 1982) was used to estimate seasonal abundance and temporary emigration probabilities. The data were organized in two hierarchical sampling periods, eight primary periods (each season was a primary period) formed by six secondary periods (each field day was a secondary period). For each primary period we estimated closed capture probabilities (p), the true encounter probability (p^* ; which is the probability of detection, given availability) and the abundance (\hat{N}) of dolphins. From the intervals between the primary sampling periods, we estimated: the apparent survival probability (Φ); the apparent encounter probability (P); the probability of temporary emigration (y'') — or being unavailable for capture, given that the individual was available during the previous sampling; and the probability that an individual emigrant remained outside the study area (y') — or unavailable for capture — during subsequent sampling (Kendall *et al.* 1995, 1997).

From the classical closed and open population models (Otis *et al.* 1978, Lebreton *et al.* 1992), we defined a set of RD models considering: the time-dependent effect between primary periods (t); time-dependent effect within primary periods (s) or between secondary periods; time-dependent effect between and within primary periods (s^*t); the cooperative group behavior effect (g); and the combination of all these effects. The cooperative group effect was included to deal with individual heterogeneity in capture probability as a result of different foraging behavior. We also explored Pledger's mixture model for heterogeneity (Pledger 2000), but found that

this model suffered from over parameterization. Behavioral response models were not included since our photo-identification procedure was not invasive. The model with no emigration ($y'' = y' = 0$) was used as a basis to investigate time-dependence and group effects. Then, we analyzed the temporary emigration probability using random (classical) and Markovian emigration models (see Kendall *et al.* 1997). To estimate parameters we used Huggins' parameterization method (Huggins 1991), which in general seems to be more stable with small sample sizes.

Model Assumptions

The assumptions for open population models (*e.g.*, CJS), include: (1) every marked animal present in the population at period x has the same probability of recapture, (2) every marked animal present at period x has the same probability of surviving to period $x + 1$, (3) marks are not lost during the study, (4) all migrations are permanent, (5) individuals are immediately released after sampling and the sampling procedure is instantaneous, and (6) the fate of marked and released animals is independent of the fate of any individual (Williams *et al.* 2002). For closed populations (the secondary periods in the RD), we should add the assumption that there is no gain or loss of marked animals during sampling from immigration or emigration, birth or death (Otis *et al.* 1978, Kendall *et al.* 1995). Violation of these assumptions causes sampling heterogeneity, a common feature of cetacean data (*e.g.*, Hammond *et al.* 1990, Evans and Hammond 2004), resulting in overdispersion, or extra binomial variation (Williams *et al.* 2002). To measure overdispersion we used our general CJS model to estimate the variance inflation factor (\hat{c}) by a parametric bootstrapping goodness-of-fit approach, with 1,000 iterations (White *et al.* 2001). Where \hat{c} was > 1 , the estimated value was used to adjust the models. Although the estimates of these adjusted models do not change, their confidence intervals get wider (Burnham and Anderson 2002). In addition, a goodness-of-fit test (TEST 2 and TEST 3 in program RELEASE, Burnham *et al.* 1987) was applied to investigate violation of assumptions (1) and (2). Although it was not investigated here, based on the short intervals within primary periods (basically 2 mo) and the high residency degree previously observed for this population, it is reasonable to assume demographic closure within these periods. We also suppose that the influence of an eventual violation of this assumption on our results may be negligible.

Model Selection Procedures

AICc (adjusted Akaike's Information Criterion) values were used to select the most parsimonious models (Anderson *et al.* 1994). As AICc behaves poorly in cases of overdispersion, when the variance inflation factor (\hat{c}) was adjusted, we used the QAICc (adjusted Quasi-likelihood Akaike's Information Criterion), which favors simpler models (Burnham and Anderson 2002). For RD models there is no goodness-of-fit (GOF) test available in program MARK (White and Burnham 1999), so again we applied the AICc method to select models. The LRT (Likelihood Ratio Test) was occasionally used to test specific biological hypotheses between nested models. We used the average of the abundance estimates across all models based on the AICc weights to take into account uncertainty in model selection (Burnham and Anderson 2002). All analyses were performed using the program MARK (White and Burnham 1999).

Total Abundance and Power Analysis

We estimated abundance for each sampling primary period (seasons) and used the group effect to estimate the abundance of cooperative dolphins (\hat{N}_1) and noncooperative dolphins (\hat{N}_2). The sum of abundance estimates per group represented the total abundance of all marked individuals ($\hat{N}_{(1+2)}$). To estimate total abundance (\hat{N}_{Total}) of bottlenose dolphins in the area, the abundance of marked individuals ($\hat{N}_{(1+2)}$) was corrected according to the proportion of marked individuals in the population (θ , see Wilson *et al.* 1999) and, the final abundance estimates were inflated according to the proportion of unmarked animals in the population ($1 - \theta$). Theta (θ) was estimated by dividing the number of marked individuals by the total number of individuals in each encountered school. We used a value of θ for each primary period averaging the θ of all schools in that period. Calves were considered as unmarked individuals. The variance of total abundance (\hat{N}_{Total}) was estimated by Delta Method following Wilson *et al.* (1999) as:

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

where n is the total number of schools (sample size) used to estimate θ . Log-normal confidence intervals for total abundance were estimated following Burnham *et al.* (1987), dividing or multiplying the total abundance by a factor C calculated as:

$$C = \exp \left[z_{\frac{\alpha}{2}} \times \sqrt{\ln\{1 + [\text{CV}(\hat{N}_{\text{Total}})]^2\}} \right] \quad (3)$$

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

We used the standard null hypothesis significance testing approach available in the program Trends (Gerrodette 1993) to conduct a power analysis in order to evaluate the sensitivity of various future monitoring scenarios to detect changes in population size (for the future, more sensible statistical techniques should be applied to assess population abundance trends; see Gerrodette 2011). These scenarios included simulated population decline (ranging from 5% to 15% declines), different estimate precision levels (using coefficients of variation (CV) of 0.05, 0.08, and 0.11), and an annual or biennial interval between monitoring surveys. In all scenarios we assumed a probability of Type I and II errors of 5% (the value routinely used by managers), used a one-tailed test (the focus here is a decreasing trend), used a CV proportional to the square root of abundance (as recommended for mark-recapture data, Gerrodette 1987), used an exponential model, and assumed a t -student distribution.

RESULTS

Photo-identification Data

We analyzed 10,209 photographs from 2007 to 2009, of which 66% were considered adequate for individual recognition. A total of 47 adults (or subadults) with long-lasting natural marks and 14 calves were identified from photographs during

Table 3. Estimates of abundance for each period from robust design models. Shown are: abundance estimates by group (\hat{N}_1 , cooperative dolphins; \hat{N}_2 , noncooperative dolphins), the sum of abundances per group ($\hat{N}_{(1+2)}$), and corrected CVs [$CV(\hat{N}_{(1+2)})$], theta (θ) estimates, the total population size adjusted by theta method (\hat{N}_{Total}), the CVs adjusted using the delta method [$CV(\hat{N}_{Total})$], the confidence intervals (\hat{N}_{Total}^L and \hat{N}_{Total}^U). Seasons: spring (Sp), summer (Su), autumn (Au), winter (Wi).

	\hat{N}_1	\hat{N}_2	$\hat{N}_{(1+2)}$	CV ($\hat{N}_{(1+2)}$)	θ	\hat{N}_{Total}	CV (\hat{N}_{Total})	\hat{N}_{Total}^L	\hat{N}_{Total}^U
Sp07	21	23	44	0.06	0.83	53	0.07	46	60
Su08	19	22	41	0.09	0.81	51	0.09	43	61
Au08	20	24	44	0.05	0.79	56	0.06	50	63
Wi08	21	25	46	0.09	0.78	59	0.10	49	72
Sp08	20	22	42	0.04	0.81	52	0.05	48	58
Su09	19	24	43	0.10	0.77	56	0.11	45	68
Au09	19	19	38	0.11	0.76	50	0.11	40	62
Wi09	18	21	39	0.08	0.74	53	0.09	45	64

was clearly promoted by cumulative sightings of new calves. The number of calves sighted was higher in the spring seasons. In total, five dolphins disappeared from our catalog and the discovery curve of new identifiable individuals within primary periods almost stabilized after the third survey day. By comparison, surveys conducted in 1989–1991 identified a total of 26 marked dolphins from 4,500 photographs (Table 1; more details in Simões-Lopes and Fabian 1999).

CJS Models

Using bootstrapping, we estimated a \hat{c} of 1.401 for the best fitting model for the recent data set. This value indicates a subtle overdispersion and we used it to adjust the models. We did not adjust models derived from Simões-Lopes and Fabian (1999) survey data since estimates of \hat{c} for were close to 1 (0.982) in this case. For all cases the results of the goodness-of-fit test indicate that we did not violate the assumption of equal capture (TEST 2) and survival (TEST 3) probabilities (TEST 2 + TEST 3 for present data: $\chi^2 = 14.469$, $P = 0.271$, $df = 12$; TEST 2 + TEST 3 for 1989–1991 data: $\chi^2 = 13.282$, $P = 0.208$, $df = 10$).

By the QAICc, the most parsimonious CJS model for the present data indicates that the estimated parameters did not vary in time and were not influenced by the group effect ($\Phi(\cdot)p(\cdot)$). This model estimated an apparent survival probability for adults and subadults of 0.979 (CI: 0.946–0.992) and an apparent capture probability of 0.865 (CI: 0.808–0.906). Then, the annual survival probability (Φ_a), derived from Φ^4 was 0.917 (CI: 0.876–0.961). For the Simões-Lopes and Fabian (1999) data, the most parsimonious model [$\Phi(\cdot)p(t)$] indicated that the apparent capture probability was significantly higher in autumn and winter seasons, varying from 0.701 to 0.928, than in summer and spring seasons, varying from 0.439 to 0.545. This time-dependence in the apparent capture probability was confirmed by the LRT [$\chi^2 = 21.928$, $P = 0.001$, $df = 6$; for model $\Phi(\cdot)p(\cdot)$ vs. $\Phi(\cdot)p(t)$]. This model estimated a survival of 0.986 (CI: 0.905–0.998), projecting an annual survival probability (Φ_a) for the period of 0.941 (CI: 0.888–0.998).

RD Models

According to AICc, the most parsimonious models had constant survival probability, Markovian or random emigration probability (with no group or time-dependence) and capture probability constant within primary periods but varying between periods and between cooperative and noncooperative groups (Table 4). This result was confirmed by LRT tests. Models with no emigration were rejected in favor of models with emigration (Random: $\chi^2 = 4,776$, $P = 0.042$, $df = 1$; Markovian: $\chi^2 = 6,206$, $P = 0.0449$, $df = 2$) and no significant difference between the emigration models was found ($\chi^2 = 2,430$, $P = 0.119$, $df = 1$). Time-dependence between periods and group effect in capture probability were significant (LRT for time-dependence: $\chi^2 = 16.318$, $P = 0.022$, $df = 7$; LRT for group effect: $\chi^2 = 31.736$, $P = 0.001$, $df = 8$) and also contributed to model fitting.

Seasonal survival probability was constant and equal to 0.980 (CI: 0.947–0.992) in the most parsimonious model (similar to the CJS estimates). The probability of temporary emigration (y'') was equal to 0.031 (CI: 0.011–0.084), while the probability of remaining outside the area (y') was 0.359 (CI: 0.053–0.847). The derived return rate of temporary emigrants ($1 - y'$) was 0.641, while the probability of remaining in the area ($1 - y''$) was 0.969. Capture probability varied between 0.299 and 0.521, and was slightly higher for the noncooperative group. However, in the autumn and winter 2008, this pattern was reversed and the capture probability increased for cooperative individuals (Fig. 2).

Total Abundance and Time to Detect a Trend

The abundance of marked dolphins using the area varied slightly throughout the study period. The highest abundance occurred in the winter 2008 (46 individuals,

Table 4. Robust design candidate models for survival probability (Φ), capture probability (p) and temporary emigration probability (y). Models are ranked by the AICc values. AICc Weight indicates how much support the selected model has over the others. Deviance is a measure of model fit. Notation: (.) constant, (t) time-dependence, (g) group effect, (y'') probability of temporary emigration, (y') probability of remained outside the study area, ($p = c$) no recapture effect, ($y'' = y' = 0$) no emigration, ($y'' = y'$) random emigration, (y''/y') Markovian emigration.

Id	Model	AICc	Δ AICc	AICc		No. parameters
				weight	Deviance	
1	$\{\Phi(.) y''(.) y'(.) p(g^*t) = c(g^*t)\}$	2,841.66	0.00	0.39	3,875.9	19
2	$\{\Phi(.) y''(.) = y'(.) p(g^*t) = c(g^*t)\}$	2,841.99	0.34	0.33	3,878.3	18
3	$\{\Phi(.) y'' = y' = 0 p(g^*t) = c(g^*t)\}$	2,843.68	2.02	0.14	3,882.1	17
4	$\{\Phi(.) y''(g) y'(g) p(g^*t) = c(g^*t)\}$	2,843.77	2.11	0.14	3,873.8	21
5	$\{\Phi(.) y''(t) y'(t) p(g^*t) = c(g^*t)\}$	2,852.98	11.33	0.00	3,863.9	30
6	$\{\Phi(.) y'' = y' = 0 p(t) = c(t)\}$	2,858.89	17.23	0.00	3,913.9	9
7	$\{\Phi(.) y'' = y' = 0 p(.) = c(.)\}$	2,861.01	19.34	0.00	3,930.2	2
8	$\{\Phi(.) y'' = y' = 0 p(g) = c(g)\}$	2,863.02	21.36	0.00	3,930.2	3
9	$\{\Phi(.) y''(g^*t) y'(g^*t) p(g^*t) = c(g^*t)\}$	2,870.40	28.74	0.00	3,852.9	43
10	$\{\Phi(.) y'' = y' = 0 p(g^*t^*s) = c(g^*t^*s)\}$	2,932.98	91.32	0.00	3,786.6	97
11	$\{\Phi(g) y'' = y' = 0 p(g^*t^*s) = c(g^*t^*s)\}$	2,935.54	93.89	0.00	3,786.6	98
12	$\{\Phi(t) y'' = y' = 0 p(g^*t^*s) = c(g^*t^*s)\}$	2,941.48	99.82	0.00	3,779.7	103
13	$\{\Phi(g^*t) y'' = y' = 0 p(g^*t^*s) = c(g^*t^*s)\}$	2,955.76	114.10	0.00	3,775.6	110

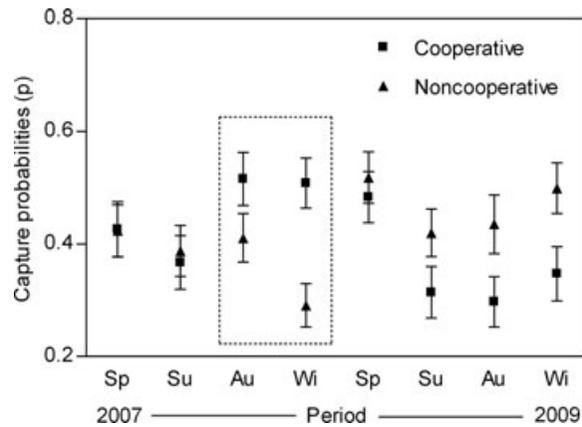


Figure 2. Variation of closed capture probabilities (p) in relation to group (cooperative and noncooperative dolphins) and seasonal (between primary periods) effects. The dotted box indicates the inversion in capture probability between groups (see text). Vertical bars represent standard errors. Periods: spring (Sp), summer (Su), autumn (Au), winter (Wi).

CV = 0.09) and the lowest occurred in the autumn 2009 (38 individuals, CV = 0.11). The highest abundance of marked noncooperative dolphins was in the winter 2008 (25 individuals), while the lowest was in autumn 2009 (19 individuals). For cooperative dolphins, highest estimates were from data collected during spring 2007 and winter 2008 (21 dolphins), and the lowest was in the winter 2009 (18 dolphins) (see Table 3). The difference between estimates of abundance of cooperative and noncooperative dolphins was higher during the summer 2009 (five individuals) and zero in the austral autumn 2009. The total population size, including animals without marks, ranged from a maximum of 59 in the winter 2008 (CI: 49–72) to a minimum of 50 individuals in the autumn 2009 (CI: 40–62) (Fig. 3; Table 3).

Our abundance estimates showed a high degree of precision. Considering a statistical power of 95% and a CV value of 0.08, we used a power analysis to estimate that it would take eight annual surveys conducted over 7 yr to detect a population decline of 5% per year, whereas six biennial surveys conducted over 10 yr are required to detect the same trend. With the higher CV of 0.11, 9 yr would be required from annual surveys and 12 yr from biennial surveys. With the lowest CV of 0.05, 6 yr would be required to detect a decline of 5% from annual surveys, and 8 yr from biennial surveys (Fig. 4). By the time a 5% decline is detected and with estimated CVs of 0.11, 37% of the original population size would be lost with annual surveys, whereas 46% would be lost with biennial surveys. For estimated CVs of 0.08, the overall decrease will be 30% by the annual effort, and 40% by the biennial effort. Finally, for estimated CVs of 0.05, a decrease of 26% will be found by an annual effort and 34% by a biennial effort.

DISCUSSION

This study provides the first robust estimates of demographic parameters for a bottlenose dolphin population in Laguna, southern Brazil. As major outcomes we highlight the small population size and the high site fidelity of these dolphins. These findings provide the cornerstone for effective conservation management of this

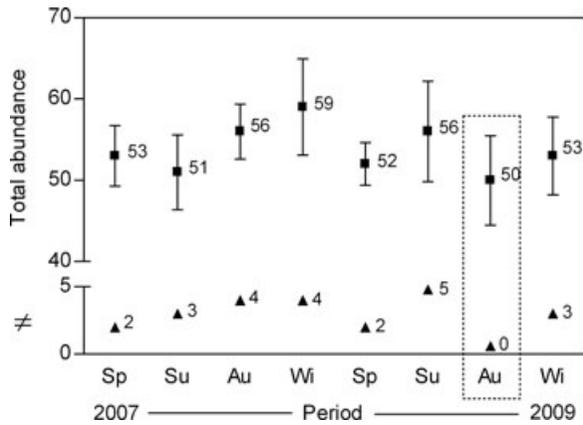


Figure 3. Variation of the total population size (squares) throughout the study, and the difference (\neq , triangles) between the abundance of noncooperative and cooperative dolphins. The dotted box indicates the low estimated total abundance in autumn 2009, when the difference between noncooperative and cooperative dolphins were null, suggesting a decreasing for this season in the number of noncooperative dolphins in the area. Vertical bars in abundance estimates represent standard errors. Periods: spring (Sp), summer (Su), autumn (Au), winter (Wi).

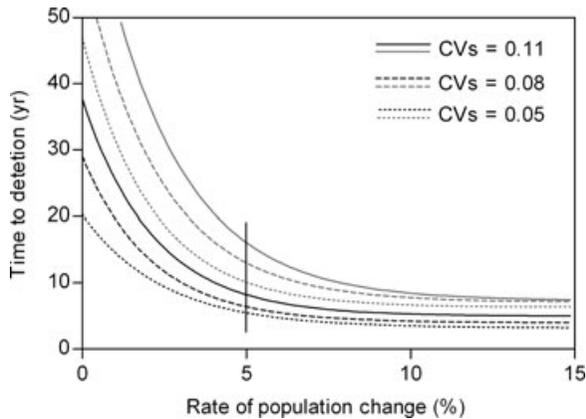


Figure 4. Relationship between rate of population change, time to detection (yr) and three possible CVs. Gray curves represent the biannual effort and black curves the annual effort. A vertical line highlights the rate of 5% of population change discussed in the text. We considered Type I and II errors at a 5% significance level and assumed exponential change.

vulnerable population, especially in the light of concerns about the preservation of a unique dolphin/human cooperative foraging strategy with local artisanal fishermen.

Abundance of Bottlenose Dolphins in Laguna

The average abundance of dolphins using the Laguna site was estimated at 54 individuals. This estimate is similar to the previous estimate of 51 individuals reported from data collected 20 yr ago (Simões-Lopes and Fabian 1999), and

appears to indicate population stability over this extended time interval ($<0.5\%$ per annum change). However, this apparent stability must be interpreted with caution due to the different sampling methods used in 1989–1991 and 2007–2009. Specifically, in the earlier study, sampling was confined to a small portion of the study area and may have consequently underestimated the abundance of animals using the whole site.

Although most coastal bottlenose dolphin populations are relatively small (Shane *et al.* 1986, Wells and Scott 1990, Wilson *et al.* 1999, Haase and Schneider 2001, Currey *et al.* 2007, Bearzi *et al.* 2008, Fury and Harrison 2008, Silva *et al.* 2009, Fruet *et al.* 2011) the resident population in Laguna appears to be one of the smallest (a population of around 30 individuals was also reported for the Estuary of Sado, Portugal, by Gaspar 2003). Although there are no data available on the productivity of the lagoon system in Laguna it is possible that the shallow waters limit prey abundance and consequently limit the carrying capacity of dolphins foraging in the site. This resource limitation could contribute to the development of alternative foraging tactics, such as the cooperation with fishermen; and if the Laguna dolphin population is small yet near carrying capacity, it may be particularly vulnerable to natural and anthropogenic habitat damage.

In general, cetacean populations of less than 100 individuals are considered to have a higher extinction risk (Thompson *et al.* 2000) and compounded by their high site fidelity these animals are particularly sensitive to local anthropogenic impacts (Sutherland 2000). Despite the apparent stability of numbers in the last 20 yr, this small and highly resident bottlenose dolphin population may be extremely vulnerable. This is especially relevant to the preservation of the unique cooperative foraging behavior which is only displayed by a small portion of the community. These animals are, potentially exposed to multiple threats such as; incidental bycatch in gill net fisheries and the cumulative effects of chemical and biological contamination—from shrimp and rice farming or from the adjacent coal mining operations. Effluent from local agriculture, aquaculture, and mining activities may have direct long-term impacts on survival and reproduction of dolphins in Laguna (Daura-Jorge and Simões-Lopes 2010) and indirect impacts through reduced habitat quality and prey abundance.

The apparent decrease in recent seasonal abundance estimates from a maximum of 59 (in the winter 2008) to a minimum of 50 (in the autumn 2009) may be related to multiple ecological factors, such as changes in the abundance mullet, changes in the ranging behavior of dolphins, and temporary emigration rather than an actual population decline. Interestingly, we noticed that the decrease in abundance during this period was mainly in the group of noncooperative dolphins, suggesting a slight foraging advantage in the dolphin-human cooperative behavior which may sustain the animals during periods of reduced prey availability. Anecdotal reports from local fishermen indicate that the abundance of mullet in the lagoon system during the cold seasons of 2008 was much higher than during the cold seasons of 2009. As the most pronounced decrease in dolphin abundance occurred during autumn 2009, it is possible that dolphins (especially the noncooperative ones) were responding to the scarcity of mullet in the area by foraging beyond the lagoon system. To confirm this hypothesis, however, focused prey surveys in and around the lagoon system are required.

Survival and Capture Probability Estimates Given by CJS

Adult annual survival probability (0.917) estimated by CJS was similar to those reported by other studies of coastal bottlenose dolphin populations which range from 0.92 to 0.97 (Wells and Scott 1990, Corkrey *et al.* 2008, Currey *et al.* 2008,

Silva *et al.* 2009). Despite being based on a short-term survey effort, this is the first attempt to estimate survival for the species in the southwestern Atlantic. Time and group effects on survival did not improve model fit, indicating there was no seasonal effect and only a slight difference between survival probabilities of cooperative and noncooperative dolphins. It should be noted however, that the relative paucity of data (seasonal estimates were based on only two years of effort) may have reduced our sensitivity to differences in survival between seasons or between foraging strategies. Although annual survival probability estimated for Simões-Lopes and Fabian (1999) data was slightly higher (0.941) than the estimates for the current period, this small difference may be an artefact of the lower number of individuals included in the capture history of the earlier study (Table 1), and not necessarily an increase in mortality rates; or due to differences in sampling efforts between periods. Continued monitoring surveys are required to determine whether an actual negative trend in survival is apparent in this population.

Apparent capture probability was also constant for the current period. Considering the cooperative behavior and its seasonality, we expected a marked difference in capture probabilities between cooperative and noncooperative dolphins and between seasons. The reanalysis of the data set from Simões-Lopes and Fabian (1999) showed this seasonal pattern and the capture probability was higher during periods with more observations of cooperative behavior (autumn and winter). This variation may have resulted from the concentration of survey effort around the interaction sites during 1989–1991 and the recent sampling methods are likely to be less sensitive to heterogeneity in capture probability resulting from foraging-cooperation affects. This was especially apparent in CJS models when entire seasons were considered as a single capture occasion whereas group effects (heterogeneity of capture probabilities due to cooperative foraging) were significant in the closed RD models.

Seasonal Emigration Rates and Other Estimates Given by RD

Although temporary emigration models fitted the data best, the emigration probability was low. Furthermore, the probability of individuals remaining in the area and the probability of emigrants returning was high. These results confirm the high site fidelity of dolphins with Laguna and the apparent geographic closure, with a low probability of immigration from neighboring communities. Indeed, it is likely that only a handful of animals account for the few records of migration between Laguna and other sites as previously described by Simões-Lopes and Fabian (1999). Survival probability given by RD models was also constant and similar to that estimated by the CJS models. This similarity is to be expected when emigration probability is low; reducing the confusion between death and emigration in the CJS models (Kendall *et al.* 1997).

The group effect showed that the closed capture probability was higher for noncooperative dolphins, but this relationship was reversed in the autumn and winter seasons of 2008. Considering the apparent high abundance of mullet during the cold season of 2008, the higher capture probabilities of cooperative dolphins during this period may be the effect of increased use of the cooperation sites to support their foraging success, while the low capture rates of noncooperative dolphins were possibly a result of these animals expanding their foraging range or adopting different foraging strategies while mullet were sparse.

Conservation and Monitoring

If this population is to be protected from threats such as gill net bycatch and environmental contaminants, management strategies and mitigation measures need to include rigorous population monitoring. Considering the lowest precision achieved during our estimates (the highest CV of our estimates was 0.11), an annual effort maintained over 9 yr will be sufficient to detect population changes in order of 5% with 95% of certainty. Since a concentrated effort with just six surveys generates precise estimates ($CV < 0.11$), we strongly suggest implementation of an annual monitoring program (Wilson *et al.* 1999) which would serve as a cost effective method to detect changes in population trends, survival probabilities, and the effect of potentially detrimental events (such as reductions in prey abundance, increased bycatch mortality or pollution events). Reducing monitoring effort to biennial surveys would save money but extend the time to detect a 5% population decline from 9 to 12 yr, resulting in a 9% increase in mortality before detection.

When high capture probabilities are obtained, a census method may be an effective and cheaper option than estimating abundance (see Currey *et al.* 2007). However, besides being more informative and providing a measure of precision, mark-recapture methods are easily applied in this case and facilitate a more robust and standardized method for future monitoring. As seasonality of foraging strategy (cooperative behavior) seems to influence capture probability, we also suggest that if mark-recapture methods continue to be used, survey effort should always be made in the same season each year for comparative purposes. Further effort may also consider the use of the newly developed mark-resight method under the robust design procedure (McClintock *et al.* 2006), which incorporates unmarked individuals directly into the modeling procedure. This approach was recently applied to data from a bottlenose population in Bangladesh (Mansur *et al.* 2011) and, if the field protocol is appropriate, it may be a useful method of combining mark-recapture procedures with photo-identification data sets.

Despite the high precision of our mark-recapture estimates and compounded by a small starting population size, our findings indicate considerable mortality is likely to be incurred before a declining population trend is detected. Therefore, we strongly recommend that a precautionary approach be adopted (Thompson *et al.* 2000), even when robust abundance estimates are reliably obtained. Population monitoring should be applied in parallel to a bycatch reduction program and habitat quality monitoring. These measures are urgently needed in order to conserve this bottlenose dolphin population and the localized cooperative behavior with artisanal fishermen, the mechanics and ecological significance of which are still poorly understood.

ACKNOWLEDGMENTS

We would like to thank Philip Hammond, who provided valuable comments and contributions at different stages of this study. FDJ thanks The Marine Institute for hosting his research visit. We also thank Leonardo Wedekin, Mauricio Cantor, and two anonymous referees for general suggestions and reviews. Finally, this study was supported by CNPq (National Counsel of Technological and Scientific Development), FAPESC (Fundação de Apoio a Pesquisa Científica do Estado de Santa Catarina), FBPN (Fundação O Boticário de Proteção à Natureza), Cetacean Society International, and Idea Wild.

LITERATURE CITED

- Anderson, D. R., K. P. Burnham and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793.
- Bearzi, G., S. Agazzi, S. Bonizzoni, M. Costa and A. Azzellino. 2008. Dolphins in a bottle: Abundance, residency patterns and conservation of bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:130–146.
- Bradford, A. L., D. W. Weller, P. R. Wade, M. B. Alexander and R. L. Brownell, Jr. 2008. Population abundance and growth rate of western gray whales *Eschrichtius robustus*. *Endangered Species Research* 6:1–14.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Springer-Verlag, New York, NY.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie and K. H. Pollock. 1987. Design and analysis of fish survival experiments based on release–recapture. American Fisheries Society Monograph No. 5. American Fisheries Society, Bethesda, MD.
- Cantor, M., L. L. Wedekin, F. G. Daura-Jorge, M. R. Rossi-Santos and P. C. Simões-Lopes. 2012. Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study. *Marine Mammal Science*. doi:10.1111/j.1748–7692.2010.00456.x.
- Chilvers, B. L., and P. J. Corkeron. 2001. Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society of London B* 268:1901–1905.
- Clavel, J., A. Robert, V. Devictor and R. Julliard. 2008. Abundance estimation with a transient model under the robust design. *The Journal of Wildlife Management* 72:1203–1210.
- Cockcroft, V. G., and G. J. B. Ross. 1990. Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of Southern Africa. *Fishery Bulletin* 88:289–302.
- Corkrey, R., S. Brooks, D. Lusseau, K. Parsons, J. W. Durban, P. S. Hammond and P. M. Thompson. 2008. A Bayesian capture-recapture population model with simultaneous estimation of heterogeneity. *Journal of the American Statistical Association* 103:948–960.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91–126 in J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. *Cetacean societies: Field studies of dolphins and whales*. The University of Chicago Press, Chicago, IL.
- Currey, R. J. C., S. M. Dawson and E. Slooten. 2007. New abundance estimates suggest Doubtful Sound bottlenose dolphins are declining. *Pacific Conservation Biology* 13:265–273.
- Currey, R. J. C., S. M. Dawson, E. Slooten, *et al.* 2008. Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: An information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:658–670.
- Daura-Jorge, F. G. 2011. Quantos? Onde? Como? Múltiplos aspectos ecológicos de uma população do boto-da-tainha (*Tursiops truncatus*) em Laguna, sul do Brasil: Implicações para a conservação [Where, how and how many? Multiple ecological aspects of a bottlenose dolphin population (*Tursiops truncatus*) in Laguna, southern Brazil: Implications for conservation]. Ph.D. thesis, Universidade Federal do Paraná, Curitiba, Brazil. 262 pp.
- Daura-Jorge, F. G., and P. C. Simões-Lopes. 2010. Lobomycosis-like disease in wild bottlenose dolphins *Tursiops truncatus* of Laguna, southern Brazil: Monitoring of a progressive case. *Diseases of Aquatic Organisms* 93:163–170.
- Evans, P. G. H., and P. S. Hammond. 2004. Monitoring cetaceans in European waters. *Mammal Review* 34:131–156.

- Fruet, P., E. R. Secchi, J. C. Di Tullio and P. G. Kinas. 2011. Abundance of bottlenose dolphins, *Tursiops truncatus*, inhabiting the Patos Lagoon estuary, southern Brazil: Implication for conservation. *Zoologia* 28:23–30.
- Fury, C. A., and P. L. Harrison. 2008. Abundance, site fidelity and range patterns of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in two Australian subtropical estuaries. *Marine and Freshwater Research* 59:1015–1027.
- Gaspar, R. 2003. Status of the resident bottlenose dolphin population in the Sado Estuary: Past, present and future. Ph.D. thesis, University of St Andrews, St Andrews, U.K. 213 pp.
- Gerrodette, T. 1987. A Power analysis for detecting trends. *Ecology* 68:1364–1372.
- Gerrodette, T. 1993. Trends: Software for a power analysis of linear regression. *Wildlife Society Bulletin* 21:515–516.
- Gerrodette, T. 2011. Inference without significance: Measuring support for hypotheses rather than rejecting them. *Marine Ecology* 32:404–418.
- Haase, P. A., and K. Schneider. 2001. Birth demographics of bottlenose dolphins, *Tursiops truncatus*, in Doubtful Sound, Fiordland, New Zealand—preliminary findings. *New Zealand Journal of Marine and Freshwater Research* 35:675–680.
- Hammond, P. S., S. A. Mizroch and G. P. Donovan. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Report of International Whaling Commission (Special Issue 12)*:135–139.
- Hoese, H. D. 1971. Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy* 52:222–223.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic models. *Biometrika* 52:225–247.
- Kendall, W. L., K. H. Pollock and C. Brownie. 1995. A likelihood based approach to capture–recapture estimation of demographic parameters under the robust design. *Biometrics* 51:293–308.
- Kendall, W. L., J. D. Nichols and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Krützen, M., J. Mann, M. R. Heithaus, R. C. Connor, L. Bejder and W. B. Sherwin. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America* 102:8939–8943.
- Lebreton, J. D., K. P. Burnham, J. Clobert and D. R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lusseau, D., K. Schneider, O. J. Boisseau, P. Haase, E. Slooten, S. D. Dawson. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations: Can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology* 54:396–405.
- Mansur, R. M., S. Strindberg and B. D. Smith. 2011. Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. *Marine Mammal Science*. doi: 10.1111/j.1748–7692.2011.00520.x.
- McClintock, B. T., G. C. White and K. P. Burnham. 2006. A robust design mark-resight abundance estimator allowing heterogeneity in resighting probabilities. *Journal of Agricultural, Biological, and Environmental Statistics* 11:231–248.
- Meurer, A. Z., and S. A. Netto. 2007. Seasonal dynamics of benthic communities in a shallow sublittoral site of Laguna estuarine system (south Brazil). *Brazilian Journal of Aquatic Science and Technology* 11:53–62.
- Otis, D. L., K. P. Burnham, G. C. White and D. R. Anderson. 1978. Statistical inference for capture data on closed animal populations. *Wildlife Monographs* 62:1–135.

- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models with heterogeneity. *Biometrics* 56:434–442.
- Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757–760.
- Pradel, R., J. E. Hines, J. D. Lebreton and J. D. Nichols. 1997. Capture–recapture survival models taking account of transients. *Biometrics* 53:60–72.
- Pryor, K., J. Lindbergh, S. Lindbergh and R. Milano. 1990. A dolphin-human fishing cooperative in Brazil. *Marine Mammal Science* 6:77–82.
- Reynolds, J. E., R. S. Wells and S. D. Eide. 2000. The bottlenose dolphin. Biology and conservation. The University Press of Florida, Gainesville, FL.
- Seber, G. A. F. 1965. A note on the multiple–recapture census. *Biometrika* 52:249–259.
- Shane, S. H., R. S. Wells and B. Würsig. 1986. Ecology, behavior and social organisation of the bottlenose dolphin: A review. *Marine Mammal Science* 2:34–63.
- Silva, M. A., S. Magalhães, R. Prieto, R. S. Santos and P. S. Hammond. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series* 392:263–276.
- Simões-Lopes, P. C. 1991. Interaction of coastal populations of *Tursiops truncatus* with the mullet artisanal fisheries in Southern Brazil. *Biotemas* 4:83–84.
- Simões-Lopes, P. C., and M. E. Fabian. 1999. Residence patterns and site fidelity in bottlenose dolphins, *Tursiops truncatus* (Montagu) (Cetacea, Delphinidae) off southern Brazil. *Revista Brasileira de Zoologia* 16:1017–1024.
- Simões-Lopes, P. C., M. E. Fabian and J. O. Menegheti. 1998. Dolphin interactions with the mullet artisanal fishing on southern Brazil: A qualitative and quantitative approach. *Revista Brasileira de Zoologia* 15:709–726.
- Sutherland, W. J. 2000. The conservation handbook: Research, management and policy. Blackwell, Hoboken, NJ.
- Taylor, M. K., J. Laake, P. D. McLoughlin, H. D. Cluff, E. W. Born, A. R. Asvid and F. Messier. 2008. Population parameters and harvest risks for polar bears (*Ursus maritimus*) of Kane Basin, Canada and Greenland. *Polar Biology* 31:491–499.
- Thompson, P. M., B. Wilson, K. Grellier and P. S. Hammond. 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Biological Conservation* 14: 1253–1263.
- Urian, K. W., S. Hofmann, R. S. Wells and A. J. Read. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science* 25:619–638.
- Verborgh, P., R. De Stephanis, S. Pérez, Y. Jaget, C. Barbraud and C. Guinet. 2009. Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* 25:523–536.
- Wedekin, L. L., F. G. Daura-Jorge, M. R. Rossi-Santos and P. C. Simões-Lopes. 2008. Notas sobre a distribuição, tamanho de grupo e comportamento do golfinho *Tursiops truncatus* (Cetacea: Delphinidae) na Ilha de Santa Catarina, sul do Brasil [Notes on the distribution, group size and behavior of the bottlenose dolphin *Tursiops truncatus* (Cetacea: Delphinidae) in the coast of the Island of Santa Catarina, southern Brazil]. *Biota Neotropica* 8(4):225–229.
- Wells, R., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture–release techniques. Report of International Whaling Commission (Special Issue 12):407–415.
- White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–138.
- White, G. C., K. P. Burnham and D. R. Anderson. 2001. Advanced features of program Mark. Pages 368–377 in R. Field, R. J. Warren, H. Okarma and P. R. Sievert, eds. *Wildlife, land, and people: Priorities for the 21st century*. The Wildlife Society, Bethesda, MD.

- Williams, J. A., S. M. Dawson and E. Slooten. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology* 71:2080–2088.
- Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, CA.
- Wilson, B., P. S. Hammond and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Würsig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. *Report of International Whaling Commission (Special Issue 12):43–52*.

Received: 28 August 2011

Accepted: 10 February 2012