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Abundance and demography of bottlenose dolphins inhabiting a subtropical estuary in the Southwestern Atlantic Ocean

PEDRO F. FRUET,* FÁBIO G. DAURA-JORGE, LUCIANA M. MÖLLER, RODRIGO CEZAR GENOVES, AND EDUARDO R. SECCHI

Programa de Pós-Graduação em Oceanografia Biológica, Universidade Federal do Rio Grande (FURG), Av. Itália Km 8, Rio Grande, RS, CEP 96201-900, Brazil (PFF)
Museu Oceanográfico "Prof. Eliézer C. Rio", Universidade Federal do Rio Grande (FURG), Rua Heitor Perdigão 10, Rio Grande, RS, CEP 96200-970, Brazil (PFF, RCG, ERS)
Laboratório de Ecologia e Conservação da Megafauna Marinha (EcoMega), Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Av. Itália Km 8, Rio Grande, RS, CEP 96201-900, Brazil (PFF, RCG, ERS)
Cetacean Ecology, Behaviour and Evolution Laboratory, School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia (PFF, LMM)
Molecular Ecology Laboratory, School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia (PFF, LMM)
Laboratório de Mamíferos Aquáticos, Universidade Federal de Santa Catarina (UFSC), Campos Reitor João David Ferreira Lima, Florianópolis, SC, CEP 88040-900, Brazil (FD-J)

* *Correspondent:* pfruet@gmail.com

We conducted a mark-recapture (MR) analysis from 8 years (2005–2012) of photo-identification data collected systematically to investigate demographic parameters of a community of bottlenose dolphins (*Tursiops truncatus*) inhabiting the Patos Lagoon Estuary and adjacent marine coast in southern Brazil. Under the most parsimonious model of Pollock's robust design, which disregarded the effects of temporary emigration, the estimate of annual apparent survival was higher for adult females (0.97, 95% *CI*: 0.91–0.99) than for adult males (0.88, 95% *CI*: 0.75–0.94) and juveniles (0.83, 95% *CI*: 0.64–0.93), which may explain an observed bias in sex ratio (1 male:2 females) of known adult dolphins in this community. An increase in abundance of marked individuals was observed during the first 6 years of sampling when the number of new recruits surpassed mortality, followed by a remarkable decrease in the last 2 years when an inverse ratio of recruits/deaths occurred. Yearly changes in abundance ($\hat{\lambda}_t$) varied from −0.1 to 0.07. Total abundance estimates were highly precise (the highest coefficient of variation was 0.053) and did not exceed 88 individuals. Abundance estimates were similar to a previous MR study conducted in the same area almost a decade earlier, suggesting a relative stable dolphin community over the last 14 years. The apparent stability in abundance, however, should be viewed with caution since this community would need a substantial mortality of at least 10% before a decline in abundance is detected with a desirable statistical power of 90%.

Key words: abundance, bottlenose dolphin, mark-recapture, power analysis, sex ratio, survival, *Tursiops truncatus*

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Reliable estimates of demographic parameters of wild populations are the baseline for understanding the population dynamics and ecology of any species, allowing for a proper assessment of the impacts of nonnatural mortality and trends in abundance (Thompson et al. 1998). Besides the intrinsic biological differences, there are many extrinsic natural factors that may cause inter- and intraspecific variability in vital parameters (e.g., survival and reproduction). For species with long lifespan and complex life history processes, survival is expected to vary according to age, sex, and an individual's genetic makeup (Ralls et al. 1980; Promislow 1992). Extrinsically, natural oscillations in ecosystem productivity (at various temporal and spatial scales) generally impact demographic parameters such as survival and fecundity rates, including for large marine vertebrates (e.g., Forcada et al. 2005; Leaper et al. 2006; Ward et al. 2009).

Relatively accurate and unbiased temporal estimates of cetacean population parameters can be obtained from longitudinal studies using data from "mark" and "recapture" (e.g., photographs of natural marks and photographic resightings) of individuals and analyzing them under a mark-recapture (MR) statistical framework (Seber 1982; Pollock et al. 1990; Kendall et al. 1995). Advances in MR analysis have enhanced the knowledge about population parameters of wild animals (see Sandercock 2006 for a review) and today analytical methods offer the opportunity to relax some assumptions and explicitly model biological conditions that were previously ignored, especially in cetacean studies (Hammond 2009).

A common problem of MR studies applied to cetaceans is the inability to survey the entire distributional range of the studied population. Movements of individuals in and out of the sampling area can occur, potentially confounding mortality with temporary or permanent emigration, which may result in imprecise and, in some circumstances, biased estimations (Kendall et al. 1997). Pollock's robust design (RD—Pollock 1982; Kendall et al. 1997), however, which combines open and closed population models in an integrated framework, explicitly deals with issues of temporary emigration and offers a more biologically sounding scenario (Smith et al. 2013).

Although the bottlenose dolphin (*Tursiops truncatus*) is one of the most-studied cetacean species, only a few studies have quantified its demographic parameters in the wild. Despite many estimates of local abundance available in the literature, long-term studies are needed to detect population trends (Currey et al. 2007; Fearnbach et al. 2012; Tezanos-Pinto et al. 2013). Survival rate, the parameter for which estimates of intrinsic population growth rate of large vertebrates is most sensitive (Caswell 2001), is rarely reported, especially when stratified by age or sex (Wells and Scott 1990; Stolen and Barlow 2003; Currey et al. 2008).

The bottlenose dolphins inhabiting the Patos Lagoon Estuary (PLE) and adjacent marine coast are part of a genetically depauperate metapopulation that are comprised of at least 5 small communities in southern Brazil, in the Southwestern Atlantic Ocean (Fruet et al. 2014). Here the term "community" refers to resident dolphins that share large portions of their ranges, socially interact with each other to a much greater extent than with dolphins in adjacent zones, and exhibit similar genetic profiles (sensu Wells et al. 1987).

Occasional fishing-related mortality of bottlenose dolphins in southern Brazil has been documented since the late 1970s. Concerns about the risk of population declines have emerged after a marked fishing-related mortality between 2002 and 2005 around PLE, primarily as a consequence of an extensive overlap with the artisanal gillnet fishery (Di Tullio 2009; Fruet et al. 2012). A proper assessment of the conservation status of these local dolphin communities requires reliable estimates of demographic parameters.

The PLE is an ideal dolphin community for MR studies due to its inshore and protected habitat as well as the large proportions of naturally marked individuals presenting high site fidelity (Dalla Rosa 1999; Fruet et al. 2011). The intensive and systematic monitoring of PLE bottlenose dolphins between 2005 and 2012, coupled with nonsystematic photo-identification data collected since 1974 (Castello and Pinedo 1977), allowed for a long-term tracking of a number of individuals, from which some vital parameters were estimated. Abundance estimates from 1998 and 2005 were around 85 individuals (Dalla Rosa 1999; Fruet et al. 2011). An analysis of long-term MR history of the PLE bottlenose dolphin community can provide baseline parameter estimates for describing its dynamics and conservation status. Therefore, the aims of this 8-year study were to 1) estimate annual abundance and examine whether the data are sufficient to detect significant trends in abundance and 2) estimate life stage and sex-specific survival rates.

MATERIALS AND METHODS

Survey design and data collection.—Between August 2005 and December 2012, boat-based surveys were conducted year-round on the core area of PLE dolphin community (Di Tullio 2009). The area sampled is 85 km^2 and encompasses the lower portion of the PLE (40 km^2) and adjacent marine coast (45 km^2). Until December 2006, surveys focused primarily in estuarine waters and followed predefined zigzag transects. Since then the surveys were extended to the adjacent marine coast and followed either zigzag or parallel-to-shore transects up to 20 km north and south of the estuary mouth (Fig. 1). After transects were surveyed, we randomly searched for dolphins in the estuary mouth (2005–2006) or along the coastal zone (2007–2012), depending on the sea conditions. Surveys were curtailed when the sea state reached Beaufort Sea states > 3. Transects were run at speeds between 18 and 22 km/h in 5.3- or 5.5-m boats equipped with a 60- or 90-hp outboard engine, respectively. Two observers positioned in the bow searched for dolphins visually. Whenever a dolphin group was sighted, the survey route was abandoned to approach the animals for photo-identification (see Fruet et al. 2011 for details). After a sufficient number of good-quality digital photographs of the dorsal fins of all presumed animals were taken, the survey was resumed.

Scoring dorsal fin photographs and individual identification.—In the laboratory, each photograph was scored with a quality grade between 1 and 3 (Q_1–Q_3—Hammond et al. 1990). Lower quality photographs (Q_2 and Q_3) were not considered for further MR analysis. "Marks" such as nicks, cuts, and deformities in the dorsal fin can persist for many years (Würsig and Würsig 1977; Würsig and Jefferson 1990). Other types of marks (e.g., tooth rakes, skin alterations) were only used to assist in differentiating individuals without long-lasting marks within each dolphin group sampled. Two trained and experienced researchers made positive resightings of cataloged individuals by comparing all the digital images. Resident dolphins were distinguishable from dolphins from other communities because marked individuals have been observed in the studied area for decades (Castello and Pinedo 1977; Fruet et al. 2011). The sighting history of each resident marked individual was translated into a numerical binary matrix of presence (1) and absence (0) for MR analysis.

Determining the sex and life stage of individuals.—The sex of individuals was determined through 1) the amplification of fragments of the SRY and ZFX genes through the polymerase chain reaction (Gilson et al. 1998) using biopsy samples (see Fruet et al. 2014), 2) by simultaneous photographs of an individual's dorsal fin marks and its genital slit, 3) from records of adult individuals repeatedly found in close association with calves, or 4) from the necropsy of carcasses of marked individuals. The longitudinal photo-id data and biological characteristics of individuals were used for determining dolphin life

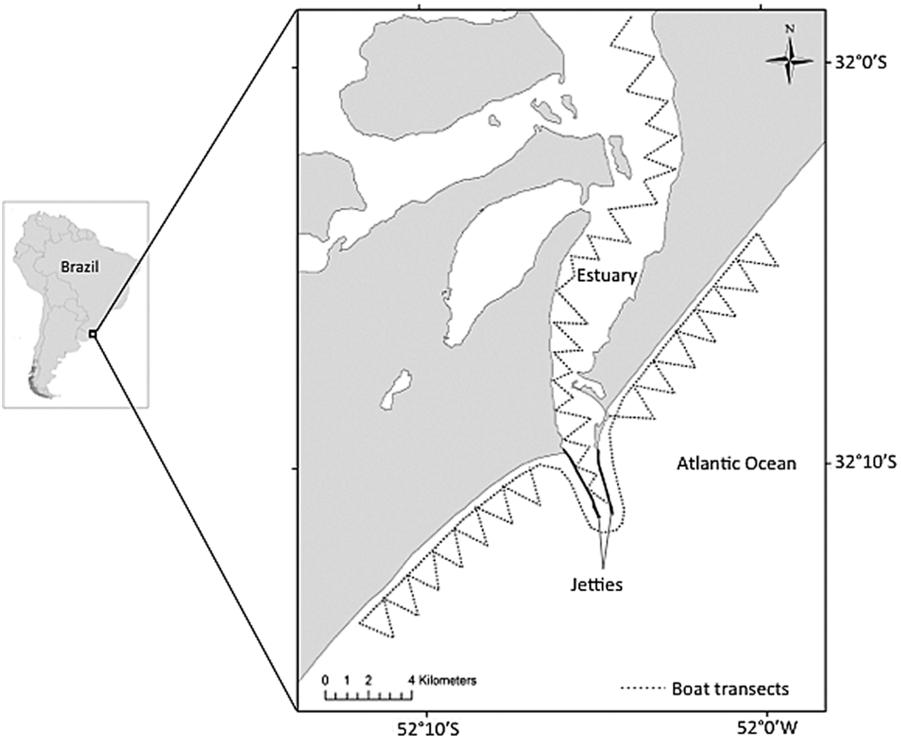

Fig. 1.—Map of the study site showing transects (dotted lines) designed for surveying bottlenose dolphins (*Tursiops truncatus*) during 2005–2012 in the Patos Lagoon Estuary and surrounding coastal areas, southern Brazil.

stages. In this study, individuals of both sexes > 7 years of age were considered adults. Although age at sexual maturation could vary between sexes (Read et al. 1993), this is close to the minimum reported age at which some individuals from PLE and other bottlenose dolphin communities from the Atlantic Ocean attain sexual maturity (Mead and Potter 1990; Wells 2000; Fruet et al. 2015). Large dolphins sighted in close association with a calf on more than 2 independent sampling occasions (days), or based on molecular sexing, were considered as adult females. Adult males in this dolphin community are distinguished from others by their larger body size (Fruet et al. 2012), notably higher dorsal fins, robustness, large number of tooth rakes on the body, and no repeatedly close association with a calf. Individuals with body size of approximately two-thirds of an adult, noticeably less robust than an adult, light-gray in coloration, and often (but not always) associated with an adult, were considered juveniles. Juveniles (between 3 and 7 years of age) used in the MR analysis acquired long-term marks in the dorsal fins during their first 2 years of life, allowing for a precise aging and tracking since separation from their mothers. All individuals (calves, juveniles, and adults) without long-term natural marks were treated as "unmarked" and included only in the analysis of the proportion of marked individuals for obtaining a total abundance estimate (see below).

MR analysis for abundance, apparent survival, and temporary emigration.—MR analysis was conducted using Pollock's RD (Pollock 1982; Kendall et al. 1997), implemented in the MARK software program version 6.2 (White and Burnham 1999). The RD combines both open and closed population models and explicitly allows for temporary emigration (Williams et al. 2002). Longer intervals among sampling periods are defined as "primary periods"—when demographic changes can occur. In contrast, the shorter sampling intervals are referred to as "secondary periods"—and assume an effectively closed unit (i.e., events of births and deaths, immigration, and emigration do not occur—Kendall et al. 1995, 1997).

As mortality and permanent emigration are confounded in MR estimates of survival, we derived apparent survival probabilities. Following the notation of Kendall et al. (1995, 1997), samples in this study were organized into 2 hierarchical periods: the primary periods were composed of 8 years with 3–4.5 months of sampling effort each year; and the secondary periods were represented by several sampling occasions within each primary period (10–13 surveys conducted between late March and early November; Table 1). This approach minimizes violation of closure assumption within primary periods since by-catch mortality and births in this area occur primarily between December and March (Fruet et al. 2012; Fruet et al. 2015). For obtaining annual parameter estimates, time intervals between primary periods were quantified as decimal years between their last and first days of sampling (Δt). Primary periods were separated by a minimum of 4.9 month (0.41 decimal years) and maximum of 12 month (Table 1). To decrease the effects of pseudoreplication (Wilson et al. 1999), data from consecutive surveys were excluded.

Model assumptions.—The following assumptions were made under the RD (following Williams et al. 2002): 1) marks were not lost during the study period; 2) marked individuals were correctly recognized when recaptured; 3) individuals were instantly released after being marked; 4) intervals between sampling occasions were longer than the duration of the sampling; 5) all individuals observed during a given sampling occasion had the same probability of surviving to the next occasion;

Table 1.—Summary of sampling scheme and survey effort for mark-recapture analysis of bottlenose dolphins (*Tursiops truncatus*) in the Patos Lagoon Estuary in southern Brazil under Pollock's robust design (see "Materials and Methods"). Δ_t = time between sampling seasons (duration of primary periods); Q_1 = number of excellent graded quality photographs; M_{t+1} = number of marked dolphins sighted.

Year	Sampling season (secondary period)	Sampling duration (month)	Number of surveys (n)	Δ_t (month)	Sampled area (km^2)	Survey effort (h:min)	Number of encounters	Q_1	M_{t+1}
2005	04 Aug. – 13 Nov.	3.4	13	6.8	40	98:21	122	1,473	56
2006	06 Jun. – 08 Oct.	4.1	12	6.1	40	96:35	118	1,469	56
2007	10 Apr. – 20 Jul.	3.4	15	8.3	85	106:48	83	1,514	58
2008	26 Mar. – 14 Jul.	3.7	11	10	85	93:20	92	1,204	58
2009	11 May – 11 Aug.	3	13	12	85	111:23	89	1,479	62
2010	06 Aug. – 05 Nov.	3	11	4.9	85	98:01	57	1,388	60
2011	01 Apr. – 06 Aug.	4.2	11	7	85	81:59	73	2,322	59
2012	03 Mar. – 17 Jul.	4.5	10		85	66:02	67	1,677	50

6) the study area did not vary geographically; 7) marked and unmarked individuals had the same probability of being captured; 8) the population remained closed (births, deaths, immigration, and emigration did not occur) within primary periods; and 9) the capture of an individual did not affect its subsequent recapture probability during the secondary period. While this sampling design likely accounted for all these assumptions, any potential violation may cause an extra binomial variation (Williams et al. 2002), which is a common characteristic of cetacean mark/recapture data (discussed later).

Building and selecting models.—The RD models contained the following parameters: ϕ = apparent survival probability between primary periods; p = probability of first capture; c = probability of recapture; γ' and γ'' = probability that an individual would be unavailable for capture during primary period t, given that it was available or unavailable, respectively, for capture in period $t - 1$ (the probability of temporary emigration), and abundance (N) which was estimated as a derived parameter by Huggins's parameterization method (Huggins 1991). We considered several statistical models to evaluate different dolphin movement patterns, considering completely random ($\gamma'' = \gamma'$) or Markovian ($\gamma' \neq \gamma''$) emigration models, or no emigration models ($\gamma'' = \gamma' = 0$) (Kendall et al. 1997). Candidate models were also constructed assuming, or not, the time dependence (t) and/or groups (g; sex and life stage) effects in the parameters of interest$\{p', p, \varphi, \gamma\}$. The most parsimonious model was selected by the AIC$_c$ (Akaike's Information Criterion adjusted for small sample size—Burnham and Anderson 2002).

In the 1st round of modeling, we ignored temporary emigration ($\gamma' = \gamma'' = 0$) and let apparent survival vary in time (t) and by group (g) to explore both time ("t" for between primary periods; "s" for within primary periods; "." constant) and group (g) effects in capture probabilities (models 9, 11, 13–15). Variation in survey effort may have affected capture probabilities in 2 ways: 1) changes in the surveyed area (in 2005/2006 surveys were carried out primarily in estuarine waters, while in subsequent years they were extended to the adjacent coastal zone) and 2) a decrease in survey effort in 2012 due to unavoidable logistical issues. To account for potential effects due to these 2 changes in sampling effort, we also built models where capture probabilities were constrained to vary between 2005–2006 and 2007–2012 seasons (p_{season}; model 10) and to vary between the 2005–2011 and 2012 (p_{2012}) seasons (model 12). For the 2nd round, we adjusted the apparent survival parameter evaluating time and group effects, considering the most parsimonious model for capture probabilities (models 1, 5, 7, 9). Then the effects of temporary emigration fitting random ($\gamma' = \gamma''$) and Markovian ($\gamma' \neq \gamma''$) models with or without time effect on these parameters were explored (models 2–4, 6, 8; Table 2). To account for model selection uncertainty, abundance estimates, and *CI*s were obtained by averaging the results from models that supported the data (Burnham and Anderson 2002). Since there are no appropriate methods available in MARK for testing the goodness-of-fit (GOF) in RD models (White and Burnham 1999), the overall model fit could not be completely evaluated. Alternatively, we collapsed our data from the secondary period of the RD and fitted Cormack–Jolly–Seber models (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992) to evaluate if the open part of the RD model fitted the data. GOF tests were run using the RELEASE program in MARK. Extra binomial variation ($\hat{c}$) was estimated by dividing the chi-square statistics of GOF tests by the number of degrees of freedom and by a parametric bootstrapping approach with 1,000 iterations. To be conservative, the higher $\hat{c}$ values were used to adjust lack of fit of the models for both approaches (cf. Silva et al. 2009). Closure assumption underlying secondary periods were verified by visual inspection of discovery curves. The plateau of the discovery curve was defined as the survey where 95% of all observed dolphins could be photo-identified.

The rates of change in population size, sex ratio of marked individuals, yearly number of recruits to the marked population, and total population size (which included the non-marked dolphins in their calculation) were computed from the same binomial dataset and/or parameters estimated by the RD modeling. Annual abundance of marked dolphins in the population was estimated separately in the RD analysis for adult females ($N1$), adult males ($N2$), and juveniles ($N3$) as derived parameters. The sum of abundance estimates per group represented the total abundance ($\widehat{N}_T$) of marked individuals ($\widehat{N}_{(1+2+3)}$). The rate of change in abundance ($\hat{\lambda}_t$) between sampling periods was calculated as:

$$\hat{\lambda}_t = \frac{N_{T(t+1)}}{N_{T(t)}}$$

Table 2.—Details of mark-recapture fitted models and model selection statistics obtained using MARK analyses of the 2005–2012 sighting history data from the Patos Lagoon Estuary bottlenose dolphin (*Tursiops truncatus*) community using the Pollock's robust design. Each model contained number of parameters (No. par.), a relative measure of fit (QDev – the relative deviance), and the quasi-Akaike's Information Criterion with a 2nd-order correction for small sample sizes ($QAIC_c$) are shown. Notation: φ = apparent survival; *p* = capture probability; (•) = constant; *t* = time dependence; *g* = group effect; γ″ = probability of temporary emigration; γ′ = probability of remaining outside the study area; (γ″ = γ′ = 0) = no emigration; (γ″ = γ′) = random emigration; γ″γ′ = Markovian emigration. Recapture probability (*c*) is not shown in the model description because it was set equal to (*p*) for all candidate models.

	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Model likelihood	No. par.	QDev
1.	$\{\phi_{(g)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(t)}\}$	4,703.64	0.00	0.44	1.00	11	5773.93
2.	$\{\phi_{(g)}\gamma'_{(\cdot)}\gamma''_{(\cdot)}p_{(t)}\}$	4,703.94	0.30	0.38	0.86	13	5770.17
3.	$\{\phi_{(g)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)}p_{(t)}\}$	4,705.68	2.03	0.16	0.36	12	5773.9
4.	$\{\phi_{(g)}\gamma'_{(g)}\gamma''_{(g)}p_{(t)}\}$	4,710.12	6.48	0.02	0.04	17	5768.2
5	$\{\phi_{(\cdot)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(t)}\}$	4,713.38	8.05	0.01	0.02	9	5775.2
6.	$\{\phi_{(g)}\gamma'_{(t)} = \gamma''_{(t)}p_{(t)}\}$	4,716.61	12.97	0.00	0.01	18	5772.6
7.	$\{\phi_{(t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(t)}\}$	4,718.11	14.46	0.00	0.00	15	5780.3
8.	$\{\phi_{(g)}\gamma'_{(t)}\gamma''_{(t)}p_{(t)}\}$	4,718.18	14.53	0.00	0.00	24	5761.8
9.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(t)}\}$	4,723.19	19.55	0.00	0.00	29	5756.5
10.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(\text{season})}\}$	4,734.11	30.46	0.00	0.00	23	5779.8
11.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(\cdot)}\}$	4,734.99	31.35	0.00	0.00	22	5782.8
12.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(2012)}\}$	4,735.34	31.69	0.00	0.00	23	5781.1
13.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(g)}\}$	4,738.31	34.67	0.00	0.00	24	5781.1
14.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(g*t)}\}$	4,747.20	43.55	0.00	0.00	45	5746.8
15.	$\{\phi_{(g*t)}\gamma'_{(\cdot)} = \gamma''_{(\cdot)} = 0p_{(g*t*s)}\}$	4,990.52	286.87	0.00	0.0000	309	5304.7

An index of recruitment and apparent mortality were obtained by determining the number of new marked individuals and disappearance of marked individuals between sampling sessions, respectively. Adult sex ratio was determined for each year.

Estimating total population size.—Total abundance of the PLE dolphin community was calculated for each year using the ratio $\frac{\hat{N}_T}{\hat{\theta}}$, where theta ($\hat{\theta}$) was the proportion of marked individuals in the population. For each primary period, $\hat{\theta}$ was estimated as: $\hat{\theta} = \frac{\sum_{i=1}^{k} \frac{I_i}{T_i}}{k}$ and its variance expressed as:

$$\operatorname{var}(\hat{\theta}) = \left(\sum_{i=1}^{k} \frac{\theta_{i(1-\theta i)}}{T_i} \right) K^2$$

where, I_i was the total number of dolphins with long-lasting marks photographed in the group *i*; T_i was the total number of dolphins photographed in group *i*; *k* was the total number of groups sampled (cf. Fruet et al. 2011).

This approach was used because marked dolphins compose a large proportion of the PLE community, mean group size was small ($\overline{X}$ = 4—Mattos et al. 2007) and superficial skin markings on the dorsal fins made it possible to distinguish individuals without long-lasting marks (unmarked) in most of sampled groups. This allowed in situ verification of photographs, thus increasing the chances that all individuals in the group were sampled. Large groups (> 8 individuals) were excluded from this analysis because the number of unmarked individuals could not be determined with certainty.

The coefficient of variation (*CV*) for the total abundance was expressed as a combination of *CV*s of $\widehat{N}$ and ($\hat{\theta}(CV(N_T) = \sqrt{(CV(\hat{N}))^2 + (CV(\hat{\theta}))^2}$), while the 95% *CI* was constructed assuming a lognormal approximation as recommended by Burnham et al. (1987).

Power analysis.—The program TRENDS (Gerrodette 1993) was used to run a power analysis to investigate the probability that the 8-year dataset would be able to detect a linear significant trend in the marked population, and also to assess the number of years required for detecting population changes with high statistical power (i.e., ≥ 90%). Three scenarios were run to simulate the detection of population decline: −5%, −10%, and −15%. We assumed a linear model (rather than exponential because there was no evidence that this dolphin community was recovering), a 1-tailed *t*-test (the focus here was on a decreasing trend), a *CV* constant with abundance (since no clear relationship was detected plotting annual *CV*s against $\sqrt{\widehat{N}}$ and $(\sqrt{\widehat{N}})^{-1}$), and a Student's *t*-distribution (Gerrodette 1987). The probability of Type I and II errors was set at 0.05 and the averaged *CV* of 3% was used to obtain the population estimates. We also evaluated the effect of increasing estimation uncertainty by increasing the *CV* to 5% (the highest *CV* obtained in this study for the total abundance estimation).

RESULTS

Photo-identification.—After selecting surveys to meet Pollock's RD model assumptions and avoid effects of pseudoreplication, data from 103 surveys were analyzed, totaling 752.5 h spent on the water photo-identifying bottlenose dolphins in the PLE and adjacent marine coast. Sampling seasons, lengths, and their respective survey effort varied across the studied period due to logistical reasons, particularly in 2012 when weather conditions limited sampling coverage. Dolphins were seen in all surveys and 701 groups were sampled (Table 1). Sightings were made throughout the study area, but most (about 72%) took place in the PLE or close to its entrance. The average group size was 5 dolphins (*SE* = 4), but groups larger than 8 individuals represented about 15% of the encounters.

A total of 21,639 photographs were analyzed, from which 13,726 photographs were graded as high quality (Q_1). The photo-id catalog used in the analysis contained 76 well-marked dolphins, including sighting histories of 18 juveniles and 58 adults (with 21 males and 37 females; Table 3). A maximum of 62 marked individuals were sighted in a single year and this number fluctuated only slightly across seasons (Table 1). The cumulative number of identified dolphins experienced a pronounced increase during the first surveys, and then gradually decreased as the survey effort progressed (Fig. 2; Supporting Information S1). New marked dolphins continually appeared at low numbers each year, resulting in an average recruitment of three individuals per year (*SD* = 2; Fig. 2). These recruits were all juveniles from known resident mothers that gained marks in the dorsal fin between sampling seasons. Most of them (95%) have subsequently returned to the study area. Resighting rates were high, with an average of 84% (*SD* = 5%) of marked dolphins subsequently sighted within, and 93% (*SD* = 4%) between sampling seasons, demonstrating high site fidelity to the area. The adult sex ratio was biased towards females in all sampling seasons (Table 4).

Table 3.—Summary of sex determination of bottlenose dolphins (*Tursiops truncatus*) from Patos Lagoon Estuary under several methodologies.

	Genetics	Photograph of genital slit	Necropsy	Parental care	Body characteristics
Male	10	0	3	0	8
Female	18	1	2	16	0

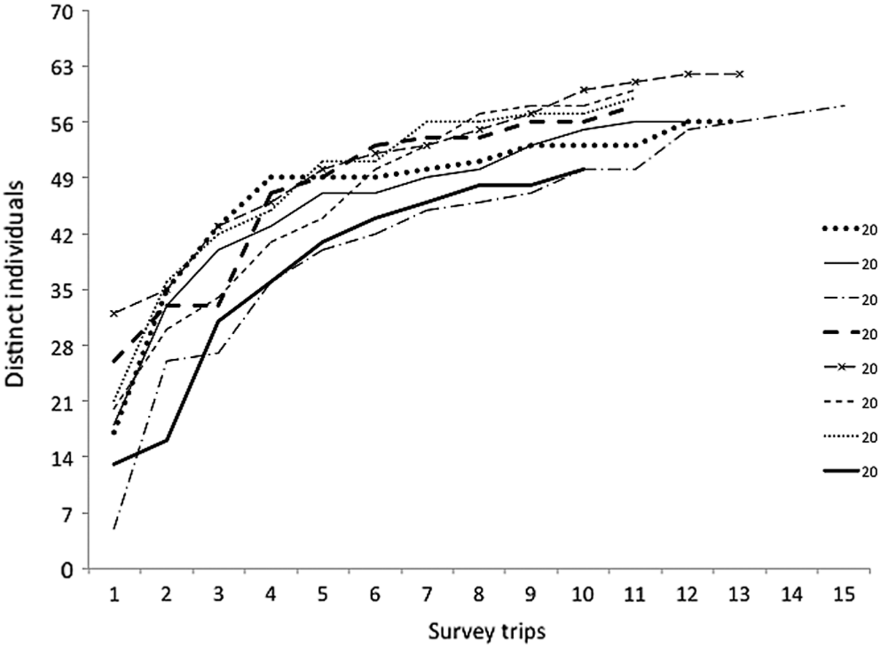

Fig. 2.—Discovery curve showing the yearly cumulative number of photo-identified bottlenose dolphins between 2005 and 2012 in the Patos Lagoon Estuary against the sequential surveys.

Table 4.—Mark-recapture parameters estimated for the Patos Lagoon Estuary bottlenose dolphin (*Tursiops truncatus*) community during 2005–2012: annual apparent survival, capture probabilities ($\hat{p}$), abundance of marked dolphins ($\hat{N}$) and their proportion in the population ($\hat{\theta}$), rate of change in abundance (λ), and annual adult sex ratio. Values in parentheses are the associated measurements of parameter estimate uncertainty.

Year	Annual constant apparent survival (95% *CI*)			$\hat{p}$ (95% *CI*)	$\hat{N}_{g1+g2+g3}$ (*CV*)	$\hat{\theta}$	λ	Adult sex ratio (M:F)
	Juveniles (*n* = 18)	Adult males (*n* = 21)	Adult females (*n* = 37)					
2005	0.83 (0.64–0.93)	0.88 (0.75–0.94)	0.97 (0.91–0.99)	0.33 (0.29–0.37)	56 (0.01)	0.69	1	17:33
2006				0.31 (0.27–0.35)	56 (0.01)	0.69	1.05	18:35
2007				0.22 (0.19–0.25)	59 (0.02)	0.72	1	20:34
2008				0.27 (0.24–0.32)	59 (0.02)	0.70	1.07	20:35
2009				0.25 (0.22–0.29)	63 (0.01)	0.72	1	18:37
2010				0.24 (0.20–0.28)	63 (0.02)	0.73	0.95	16:37
2011				0.28 (0.24–0.32)	60 (0.02)	0.68	0.90	16:35
2012				0.22 (0.18–0.27)	54 (0.03)	0.69		13:31

GOF test and c-hat adjustment.—The GOF test showed that the assumption of equal capture (TEST 2) and survival (TEST 3) probabilities were not violated and that the global Cormack–Jolly–Seber model fitted the data well (TEST 2 + TEST 3; $\chi^2 = 11.318$, $p = 0.254$, *d.f.* = 9). Indeed, when estimating c-hat with RELEASE (= 1.25), and the Bootstrapping approach (= 1.42), no significant overdispersion was detected. Adjusting the models by the higher estimated c-hat did not change AIC$_c$ ranking but redefined models weight, which in turn slightly modified the parameters estimated by the model averaging procedure.

Model selection.—Quasi-AIC with a 2nd-order correction for small sample sizes (QAIC$_c$) values indicated that during the first round of modeling, the most parsimonious model (model 9), which disregarded temporary emigration and considered time variation between primary periods on the capture probability, fitted the data better than models allowing for a series of variation in capture probabilities, including group effects (models 11, 13, and 14). Models incorporating potential effects of sampling effort (models 10 and 12) also had a poor fit (Table 2).

For the 2nd round of modeling, the best-fitting model considered no time dependence and group effect in survival probabilities, with no temporary emigration and with time-dependent capture probabilities among primary periods (model 1). A model considering Markovian constant temporary emigration (model 2) also adequately fitted the data (ΔQAIC$_c$ < 2; Table 2). Models considering temporary emigration, however, did not provide adequate parameter estimation (unrealistic *CI*s and upward biased survival), and therefore results from these models were not considered further.

Apparent survival and capture probabilities.—Overall apparent survival (considering model 5 that disregarded the group effect in survival) was 0.93 (95% *CI*: 0.89–0.95). Nevertheless, when considering the best fitted model, which takes into account group effect, the average annual apparent survival estimate was higher for adult females (0.97, 95% *CI*: 0.91–0.99) than for adult males (0.88, 95% *CI*: 0.75–0.94) and juveniles (0.83, 95% *CI*: 0.64–0.93). Mean annual capture probabilities among primary periods were moderate, with the highest obtained during 2005 season (0.33), and the lowest in 2007 (0.22; Table 4).

Trends in abundance and power analysis.—Within each primary period, the plateau of the discovery curve was reached before the final survey (Fig. 2). Marked population size estimations were highly precise (*CV*s from 0.8% to 3.2%) and fluctuated around 50–60 individuals during the study period (Figs. 3 and 4). An increase in abundance was observed during the first 6 years of sampling, followed by a decrease in the last 2 years. Yearly changes in abundance ($\hat{\lambda}_t$) varied from −10% to 7% and were most evident from the highest number of 63 dolphins in 2010 to the lowest of 54 at the end of the sampling period (Table 4; Fig. 3).

Despite the high precision obtained to estimate the number of marked individuals in the community (*CV* = 0.03), power analysis showed that small changes in abundance (−5%) could not be statistically detected over short periods of time. Nevertheless, our 8 years of monitoring provided a satisfactory power of 0.89 and 1.00 to detect an overall population decline of 10% and 15%, respectively (Fig. 5). An additional 3 years of sampling effort would provide a desirable 0.95 likelihood of detecting a 10% decline in population size. However, a slight increase in abundance uncertainty (*CV* = 0.05) greatly inflated the minimum number of years required to detect a negative trend under the target power of 90% (Fig. 5).

Mark rate and total abundance.—The estimated proportion of marked dolphins in the PLE community remained relatively stable over the years, ranging from 0.68 to 0.72 (Table 4), exerting a small influence in the total abundance variation (Fig. 3). The highest proportions of marked animals were estimated for years with the highest recruitment of juveniles into the marked population (2007, 2008, and 2009). Total abundance ranged from 78 (95% *CI* = 70–86) in 2012 to 88 (95% *CI* = 82–94) in 2011, and even considering the highest of all upper confidence limits, maximum abundance did not exceed 94 dolphins.

DISCUSSION

This work represents one of the very few longitudinal studies designed for estimating demographic parameters for bottlenose dolphins along the Southwestern Atlantic Ocean. It differed from others by its consistent survey effort throughout an 8-year period and by deriving life stage and sex-specific apparent

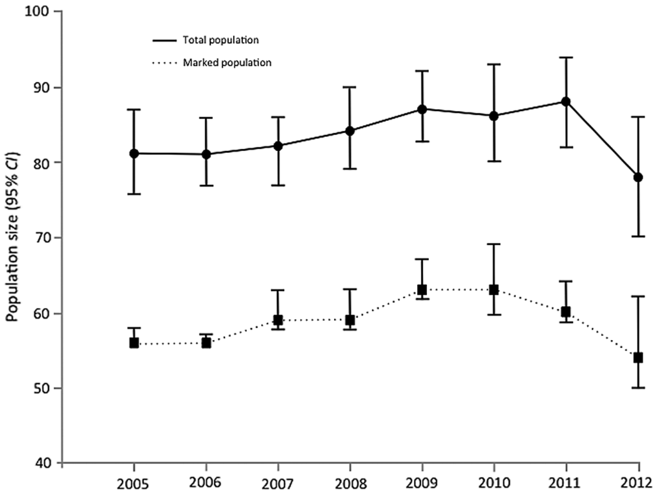

Fig. 3.—Annual abundance estimates for the Patos Lagoon Estuary bottlenose dolphin (*Tursiops truncatus*) community in 2005–2012 and their associated levels of uncertainty. Dashed and continuous lines are estimates for marked and total population size (corrected by the proportion of marked individuals in the population), respectively. Vertical lines are the 95% *CI*s.

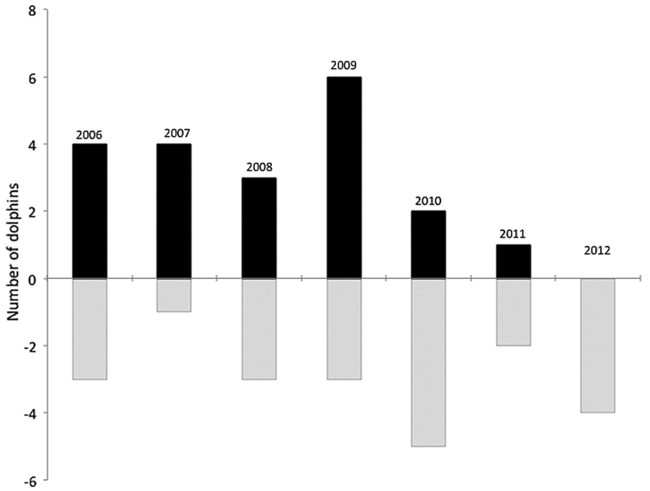

Fig. 4.—Gross annual recruitment (black bars above the x-axis) and apparent mortality (gray bars, below the x-axis) extracted from the 2005–2012 sighing history data of naturally marked resident bottlenose dolphins (*Tursiops truncatus*) from the Patos Lagoon Estuary, southern Brazil.

survival probabilities. The results suggested that the PLE dolphin community was female-biased and relatively stable during the study period, despite the reported incidental mortality in fisheries for the last decade in adjacent areas (between 2002 and 2006, minimum number of by-caught bottlenose dolphins was 21—Fruet et al. 2012). The high adult female apparent survival contrasted with the relatively poor apparent survival of adult males and juveniles, possibly reflecting a combination of natural mortality and distinct vulnerability of these population components to entanglement in gillnets.

RD model assumptions.—Closure assumption was supposedly met by using data yearly collected on the main distribution area of the PLE dolphin community over a relatively short time (considering that bottlenose dolphins can live for more than 4 decades—Wells and Scott 1999—4 months would represent only 1% of their life time), and during a period when the probability of human-induced mortality and births were low (Fruet et al. 2012). This is supported by the discovery curves and high resighting rates of marked dolphins within primary periods, which suggest a closed unit within sampling seasons and that nearly all marked individuals in the PLE community were captured during the study.

Effects of individual heterogeneity could not be properly evaluated because Pledger's mixture model (Pledger 2000) suffered from overparameterization. However, systematically covering the entire sampling area, stratifying data by dolphin sex and life stage, and using only well-marked animals for MR analysis should have reduced the effects of heterogeneity. In addition, the results of GOF tests did not suggest heterogeneity and the overdispersion estimates were not outstanding.

Capture probabilities, temporary emigration, and survival.—In many mammal species, including some communities of a closely related species, the Indo-Pacific bottlenose dolphin (*T. aduncus*), females tend to remain with their natal groups, whereas males are more likely disperse or to travel longer distances (Möller and Beheregaray 2004). The MR modeling reported herein, however, revealed that group had a nonsignificant effect on both temporary emigration and capture probabilities, which would be expected in case of a substantial variation in habitat preferences and dispersal between sexes or life stages. This, together with the high resighting rates of individuals within and between sampling periods demonstrate marked fidelity to the study area and the importance of the PLE and surrounding areas for this bottlenose dolphin community.

The overall apparent adult survival rate estimated herein (0.93; 95% *CI*: 0.89–0.95) was similar to those reported for other wild coastal communities of bottlenose dolphins (e.g., Sarasota Bay, United States of America [0.96 ± 0.01 *SD*] by Wells and Scott 1990, in Doubtful Sound, New Zealand [0.94, 95% *CI*: 0.92–0.95] by Currey et al. 2008, and at the nearby community of Laguna, southern Brazil [0.92, 95% *CI*: 0.88 – 0.96] by Daura-Jorge et al. 2013). Differences in survival estimates are likely to reflect differences in ecological characteristics of the study sites (Currey et al. 2008). Variations could also be due to unevenly sampled ages to derive adult survival, and/or different levels of human-induced impacts (Silva et al. 2009).

One of the important features of this study was the ability to estimate sex- (for adults only) and age-specific (adults and juveniles) apparent survival rates. These stratified estimates represent an advance for understanding processes shaping the dynamics of a bottlenose dolphin community. Models with group effect were strongly supported, from which constant apparent survival rates for juveniles (0.83, 95% *CI*: 0.64–0.93), adult males (0.88, 95% *CI*: 0.75–0.94), and females (0.97, 95% *CI*: 0.91–0.99) were estimated.

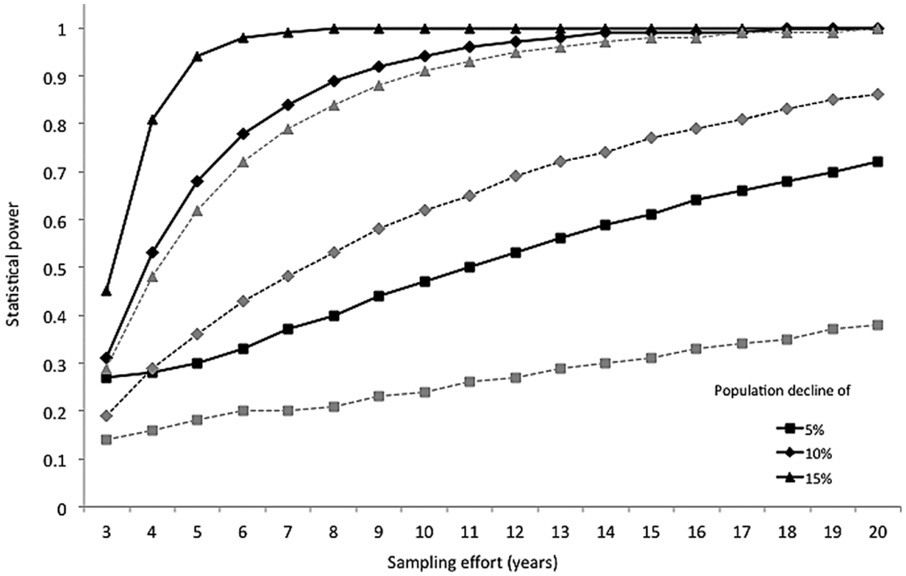

Fig. 5.—Plot of power analysis showing the relationship between statistical power and time (represented as sampling effort) to detect a significant overall population decline of 5%, 10%, and 15% in the face of 2 levels of precision found during the 8 years (2005–2012) of monitoring a population of bottlenose dolphins (*Tursiops truncatus*) in Patos Lagoon Estuary, southern Brazil: the average ($CV = 0.03$—black, continuous line) and highest (CV of 0.05—gray, dashed lines). For this analysis, we assumed a linear model, a 1-tailed test, a CV constant with abundance, and a t-student distribution, fixing the probability of Type I and II errors as 0.05.

Life history strategy should be considered as a potential source of intraspecific disparate survival rates. Bottlenose dolphins from the PLE are known to be sexually dimorphic, with males reaching larger sizes than females (Fruet et al. 2012). In sexually dimorphic species with a polygynous mating system, survival is expected to vary by sex due to differential energy investment in growth and reproduction (i.e., male aggressive behavior towards other conspecifics for mating access might constrain male survival—e.g., Ralls et al. 1980; Promislow 1992; Read et al. 1993). In the case of juveniles, we have no evidence that this stage class is subject to different force of natural mortality compared to adults. Predation, for which juveniles could be more susceptible, seems not to be an important source of mortality for this community (Fruet et al. 2012). Neither systematic or nonsystematic long-term photo-identification surveys have detected any dolphin with scars that would indicate attempt of predation.

Sex and life stage biases in by-catch mortality are certainly an important factor influencing apparent survival estimates for the PLE bottlenose community. Analysis of a dataset consisting of carcasses recovered during systematic beach surveys carried out between 1974 and 2006 in this region has shown that mortality of bottlenose dolphins near PLE was relatively high for immature and adult males (Fruet et al. 2012). This mortality pattern corroborates the apparent survival estimates in this study and likely relates to the skewed female sex ratio of live adult dolphins during the present study (approximately 1 male:2 females—see also Fruet et al. 2014). Similar skewed female sex ratio was found for Sarasota bottlenose dolphins (Wells et al. 1987).

The lower vulnerability of females to entanglement in our study area has yet to be determined. Fishing net densities were higher in the coastal areas adjacent to the entrance of the PLE (Di Tullio 2009) and the sex ratio of biopsied dolphins (marked and unmarked individuals) inside the estuary was skewed towards females—Fruet et al. 2014). In contrast, both juvenile and adult male bottlenose dolphins might have larger home ranges (e.g., Wells et al. 1987; Scott et al. 1990; Quintana-Rizzo and Wells 2001) that might also increase susceptibility to fatal interactions with fisheries. In addition, the inexperience of juveniles may enhance chances of entanglement. Several studies have reported high juvenile bottlenose dolphin mortality associated with human interactions such as fisheries and boat strikes (Wells et al. 1987; Hersh et al. 1990; Wells and Scott 1997; Stolen and Barlow 2003). Therefore, overlap between the distribution of fishing nets and female bottlenose dolphins was probably lower compared to adult males and juveniles. Differentiating nonnatural (by-catch) from natural mortality would allow for explicitly testing a wide range of biological hypotheses for these differences in survival rates. Individual genetic tagging of marked individuals (i.e., double tagging—e.g., Carrol et al. 2011) offers a promising alternative to verify whether or not stranded carcasses of by-caught dolphins belonged to the marked population, once the recognition of natural marks in the dorsal fin is often impaired due to carcass condition.

Abundance estimates and trends.—The abundance estimates were highly precise and confirmed the small size of the PLE dolphin community found in previous studies (Dalla Rosa 1999; Fruet et al. 2011). Communities of bottlenose dolphins associated with coastal, protected habitats, such as estuaries and river mouths, are generally small and residents or semiresidents (e.g., Wells and Scott 1990; Currey et al. 2007), but they tend to increase in numbers and range when inhabiting primarily open coasts (e.g., Defran and Weller 1999; Gubbins et al. 2003). In southern Brazil and Uruguay, small communities of bottlenose dolphins < 90 individuals seem to be common in both relatively protected habitat and open coast (Fruet et al. in press).

As in a large number of populations of long-lived vertebrates (Caughley and Sinclair 1994), the annual rate of increase fluctuated only slightly over this long-term study, with no obvious changes in population size. Observed shifts in total abundance were closely associated with number of recruits to, and disappearances from, the marked population between primary periods. Lowest and highest abundance estimates were obtained immediately following high and low annual mortality rates during summer months, respectively. Records from stranding carcasses systematically collected along the surveyed area during 2005–2012 also corroborated the observed inverse relationship between mortality and abundance. These findings suggest that fluctuations in total abundance were not only due to sampling variation (or movement in and out of the study area), but also to nonnatural mortality that is possibly affecting the dynamics of this dolphin community. In addition, when mortality rates were low, abundance estimates increased, suggesting that PLE community may have a solid resilience under its current age and sex structure.

The abundance estimates and associated precision were similar to a previous MR study carried out with the PLE dolphin community in 1998 ($N_T = 83$ [79–88]; M_{th} model—Dalla Rosa 1999). This suggests a stable community over the last 15 years, and that the Patos Lagoon Estuary still provides a healthy ecosystem for bottlenose dolphins even in the face of substantial ecological changes as a result of overfishing and habitat degradation (Moraes et al. 2012). Given the importance of mature females for reproduction and population viability, the high estimated survival rate of this component was probably the main factor buffering against the effects of nonnatural mortality in the dynamics of this dolphin community. Alternatively, this dolphin community could be going through a very slow process of decline, which may require a longer data set, or increased effort, to detect significant changes in abundance with high statistical power.

Future research.—Viability of small demographically independent units is naturally constrained due to environmental and demographic stochastic factors (Caswell 2001) and can be seriously jeopardized if survival is reduced by nonnatural factors, such as by-catch or catastrophic disease epidemics. The long-term monitoring of PLE bottlenose dolphin community is particularly important because the Brazilian government has recently approved a fishing closure area in the southern portion of the PLE and adjacent marine coast. This closure, which includes the core area used by this dolphin community, was specifically designed for banning gillnets in places of high overlap between dolphins and fisheries (Di Tullio 2009). Thus, the continued monitoring of PLE dolphins in future years will provide data for quantifying and assessing the effectiveness of this conservation measure. This long-term monitoring will also increase the likelihood of detecting trends in abundance and thus allowing for an understanding of how this dolphin community may respond to environmental stress. Other demographic parameters, such as age at first reproduction, fecundity, calf survival, and longevity should be prioritized in future research. These parameters are relevant for building age-structured population models to describe the dynamics of this community and assessing its viability in the face of current and future human impacts and environmental change.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Discovery curve plot showing the cumulative number of photo-identified bottlenose dolphins in the Patos Lagoon Estuary against the sequential survey effort and the respective number of individuals sighted during each survey.

LITERATURE CITED

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference. Springer-Verlag, New York.

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.

Carrol, E. L., N. J. Patenaude, S. J. Childerhouse, S. D. Kraus, R. M. Fewster, and C. S. Baker. 2011. Abundance of the New Zealand subantarctic southern right whale population estimated from photo-identification and genotype mark-recapture. Marine Biology 158:2565–2575.

Castello, H. P., and M. C. Pinedo. 1977. Botos na Lagoa dos Patos. Natureza em Revista 12:46–49.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Scientific Publications, Boston, Massachusetts.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

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., 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.

Dalla Rosa, L. 1999. Estimativa do tamanho da população de botos, *Tursiops truncatus*, do estuário da Lagoa dos Patos, RS, a partir da foto-identificação de indivíduos com marcas naturais e da aplicação de modelos de marcação-recaptura. M.Sc. thesis, Universidade Federal do Rio Grande, Rio Grande, Brazil.

Daura-Jorge, F., S. N. Ingram, and P. C. Simões-Lopes. 2013. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. Marine Mammal Science 29:293–311.

Defran, R. H., and D. W. Weller. 1999. Occurrence, distribution, site fidelity and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. Marine Mammal Science 15:366–380.

Di Tullio, J. C. 2009. Uso do habitat do boto, *Tursiops truncatus*, no estuário da Lagoa dos Patos e águas costeiras adjacentes, RS, Brasil. M.Sc. thesis, Universidade Federal do Rio Grande, Rio Grande, Brazil.

Fearnbach, H., J. Durban, K. Parsons, and D. Claridge. 2012. Photographic mark-recapture analysis of local dynamics within an open population of dolphins. Ecological Applications 22:1689–1700.

Forcada, J., P. N. Trathan, K. Reid, and E. J. Murphy. 2005. The effects of global climate variability in pup production of Antarctic fur seals. Ecology 86:2408–2417.

Fruet, P. F., E. R. Secchi, J. C. Di Tullio, and P. G. Kinas. 2011. Abundance of bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae), inhabiting the Patos Lagoon estuary, southern Brazil: implications for conservation. Zoologia 28:23–30.

Fruet, P. F., et al. 2012. Temporal trends in mortality and effects of by-catch on common bottlenose dolphins, *Tursiops truncatus*, in southern Brazil. Journal of Marine Biological Association of United Kingdom 92:1865–1876.

Fruet, P. F., et al. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics 15:879–895.

Fruet, P. F., P. A. C. Flores, and P. Laporta. In press. Report of the working group on population parameters and demography of *Tursiops truncatus* in the Southwestern Atlantic Ocean. Latin American Journal of Aquatic Mammals.

Fruet, P. F., R. C. Genoves, L. M. Möller, S. Botta, and E. R. Secchi. 2015. Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. Marine Biology 162:661–673.

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.

Gilson, A., M. Syvanen, K. F. Levine, and J. D. Banks. 1998. Deer gender determination by polymerase chain reaction: validation study and application to tissues, bloodstains, and hair forensic samples from California. California Fish and Game 84:159–169.

Gubbins, C. R., M. Caldwell, S. G. Barco, K. Rittmaster, N. Bowles, and V. Thayer. 2003. Abundance and sighting patterns of bottlenose dolphins (*Tursiops truncatus*) at four northwest Atlantic coastal sites. Journal of Cetacean Research and Management 5:141–147.

Hammond, P. S. 2009. Mark-recapture. Pp. 705–709 in Encyclopedia of marine mammals (W. F. Perrin, B. Würsig, and J. G. M. Thewissen, eds.). Academic Press, San Diego, California.

Hammond, P. S., S. A. Mizroch, and G. P. Donovan (eds.) 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12. International Whaling Commission, Cambridge, England.

Hersh, S. L., D. K. Odell, and E. D. Asper. 1990. Bottlenose dolphin mortality patterns in the Indian/Banana River system of Florida. Pp. 155–164 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

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., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

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.

Leaper, R., J. Cooke, P. Trathan, K. Reid, V. Rowntree, and R. Payne. 2006. Global climate drives southern right whale (*Eubalaena australis*) population dynamics. Biology Letters 2:289–292.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Mattos, P. H., L. Dalla Rosa, and P. F. Fruet. 2007. Activity budgets and distribution of bottlenose dolphins (*Tursiops truncatus*) in the Patos Lagoon estuary, southern Brazil. Latin American Journal of Aquatic Mammals 6:161–169.

Mead, J. G., and C. W. Potter. 1990. Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pp. 165–195 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

Möller, L. M., and L. B. Beheregaray. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Molecular Ecology 13:1607–1612.

Moraes, L. E., E. Paes, A. Garcia, O. Möller, Jr., and J. Vieira. 2012. Delayed response of fish abundance to environmental changes: a novel multivariate time-lag approach. Marine Ecology Progress Series 456:159–168.

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.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–97.

Promislow, D. E. L. 1992. Costs of sexual selection in natural population of mammals. Proceedings of the Royal Society of London, B. Biological Sciences 247:203–210.

Quintana-Rizzo, E., and R. S. Wells. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into organization. Canadian Journal of Zoology 79:447–456.

Ralls, K., R. L. Brownwell, and J. Ballou. 1980. Differential mortality by sex and age in mammals with specific reference to the sperm whale. Report of the International Whaling Commission, Special Issue 2:233–243.

Read, A. J., R. S. Wells, A. A. Hohn, and M. D. Scott. 1993. Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. Journal of Zoology (London) 231:107–123.

Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504–1520.

Scott, M. D., R. S. Wells, and A. B. Irvine. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. Pp. 235–244 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

Seber, G. A. F. 1965. A note on the multiple–recapture census. Biometrika 52:249–259.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. The Blackburn Press, London, United Kingdom.

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.

Smith, H. C., K. Pollock, K. Waples, S. Bradley, and L. Bejder. 2013. Use of the Robust Design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. PLoS One 8:e76574.

Stolen, M. K., and J. Barlow. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon System, Florida, USA. Marine Mammal Science 19:630–649.

Tezanos-Pinto, G., et al. 2013. Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. Marine Mammal Science 29:390–410.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California.

Ward, E. J., E. E. Holmes, and K. C. Balcomb. 2009. Quantifying the effects of prey abundance on killer whale reproduction. Journal of Applied Ecology 46:632–640.

Wells, R. S. 2000. Reproduction in wild bottlenose dolphins: overview of patterns observed during a long-term study. Pp. 57–74 in Bottlenose Dolphins Reproduction Workshop Report (T. Duffield and T. Robeck, eds.). Silver Springs, Maryland.

Wells, R. S., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Pp. 407–415 in Reports of the International Whaling Commission, Special Issue 12 (P. S. Hammond, S. A. Mizroch, and G. P. Donovan, eds.). International Whaling Commission, Cambridge, England.

Wells, R. S., and M. D. Scott. 1997. Seasonal incidence of boat strikes of bottlenose dolphin near Sarasota, Florida. Marine Mammal Science 13:475–480.

Wells, R. S., and M. D. Scott. 1999. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). Pp. 137–182 in Handbook of marine mammals. The second book of dolphins and the porpoises (S. H. Ridgway and R. Harrison, eds.). Academic Press, San Diego, California.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pp. 247–305 in Current mammalogy (H. Genoways, ed.). Plenum Press, New York.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

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 M. Würsig. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755–756.

Würsig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameter. Pp. 43–52 in Reports of the International Whaling Commission, Special Issue 12 (P. S. Hammond, S. A. Mizroch, and G. P. Donovan, eds.). International Whaling Commission, Cambridge, England.

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