

Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA

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ABSTRACT

The stock structure of western North Atlantic bottlenose dolphins (*Tursiops truncatus*) is complex, with seasonally migratory stocks often overlapping with year-round resident stocks. High rates of exchange between northernmost sites have been documented but movement and seasonal fluctuation in abundance among sites along the southern portion of the US Atlantic coast is not well understood. To better understand seasonal abundance, a three-year mark-recapture study of bottlenose dolphins in coastal and estuarine waters near Charleston, South Carolina, USA was conducted. A robust design was employed in order to minimise bias and more precisely determine seasonal estimates of abundance and concurrently examine temporary immigration/emigration and survivorship. Systematic boat-based surveys were carried out ($n = 192$) from January 2004 to December 2006. The entire study area was surveyed one week per month; an additional survey was conducted in the months in which seasonal abundance was estimated: January (winter), April (spring), July (summer) and October (autumn). Standard photo-identification techniques were used to accumulate sightings of 521 distinctively marked dolphins, 65% of which were sighted more than once. Pollock's robust design was applied using *MARK* and the ensuing abundance estimates were adjusted for the seasonal proportion of unmarked dolphins (ranging from 0.27 to 0.40) in the population. Estimates ranged from 364 (95% CI = 305–442) in January 2004 to 910 (95% CI = 819–1018) in October 2006. Summer abundance estimates were consistently greater than those from winter months, although estimates varied considerably among years. The same model was used to calculate an annual survival rate estimate of 0.951 (95% CI = 0.882–1.00) for marked individuals within the population. A high degree of transience, demonstrated by seasonal influxes of single-sighted individuals, made it difficult to differentiate between mortality and permanent emigration. The results support the occurrence of three distinct dolphin groups found in Charleston waters: year-round residents; seasonal residents; and transients. Reporting abundance and survivorship estimates together is useful in explaining and validating results for populations in which transient individuals occur. These results provide important information for stock and viability assessment of coastal bottlenose dolphins in the western North Atlantic.

KEYWORDS: BOTTLENOSE DOLPHIN; PHOTO-ID; SURVIVORSHIP; ABUNDANCE ESTIMATE; MARK-RECAPTURE; NORTH AMERICA; NORTHERN HEMISPHERE

INTRODUCTION

Limited published accounts exist on the abundance and survival of bottlenose dolphins (*Tursiops truncatus*) from the eastern coast of the United States. While previous studies (Barco *et al.*, 1999; Read *et al.*, 2003) have reported abundance estimates for bottlenose dolphins in localised areas, to date Read *et al.* (2003) have provided the only estimate for estuarine dolphins included in the most recent NMFS stock assessment (Waring *et al.*, 2009). Similarly, to our knowledge only one published report (Stolen and Barlow, 2003) provides estimates of annual mortality rates from strandings of US east coast bottlenose dolphins.

Bottlenose dolphins have been identified for decades using natural markings (Caldwell, 1955). Individual recognition through photographs, a process known as photo-id, has become the recognised tool for tracking small cetaceans over time (Würsig and Jefferson, 1990). These markings, primarily in the thin connective tissue of the trailing edge of the dorsal fin, may last throughout a dolphin's lifetime and can be used to identify and monitor individuals (i.e. 'capture' an individual dolphin) (Irvine *et al.*, 1982; Lockyer and Morris, 1990; Read *et al.*, 2003;

Würsig and Jefferson, 1990). In general, fins are considered distinctive or 'marked' if they contain a readily identifiable feature (e.g. a mutilated fin) or intermediate features (e.g. fins with at least two distinguishing or one major feature) that are recognisable over time (Friday *et al.*, 2000). Given that mark-recapture requires accurate identification of individuals within a population, correct identification and cataloguing of fins is crucial to obtaining unbiased estimates (Friday *et al.*, 2000; Read *et al.*, 2003; Würsig and Jefferson, 1990).

Photo-id research on bottlenose dolphins near Charleston, SC began in October 1994, where Zolman (2002) documented year-round residents in the Stono River estuary (SRE). Effort was eventually expanded to adjacent areas (i.e. Charleston Harbor and coastal waters). Speakman *et al.* (2006) identified 839 distinctive individuals from 1994–2003. In addition to residents, dolphins that appeared to be infrequent, short-term visitors (i.e. transients) to the study area were identified. Herein, photo-id data collected from 2004–06 and mark-recapture techniques are used to model both survivorship and seasonal abundance of dolphins near Charleston.

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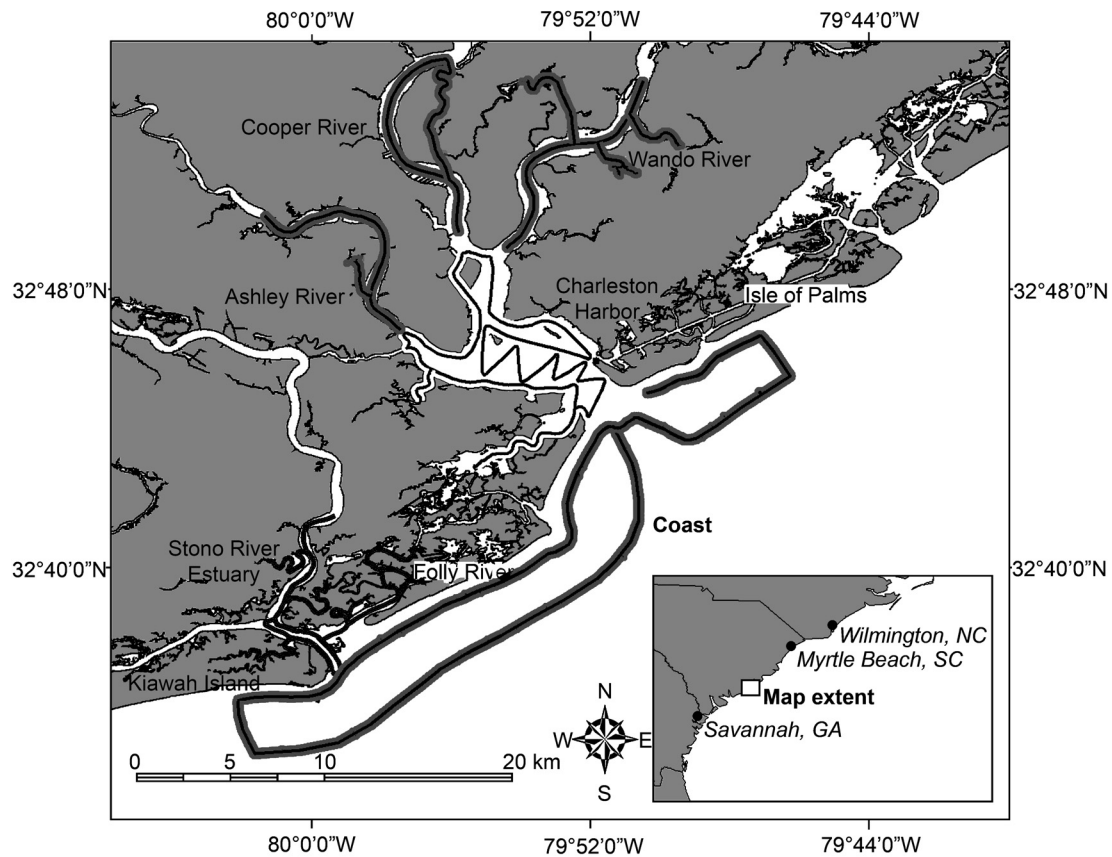


Fig. 1. Charleston, SC study area with survey routes.

METHODS

Study area and field effort

The study area is comprised of four regions in estuarine and coastal waters near Charleston, SC ($32^{\circ}40'N$, $79^{\circ}55'W$; Fig. 1):

- (1) SRE: the southernmost region is comprised of the main channel and creeks of the lower Stono River estuary, including portions of the Kiawah and Folly rivers;
- (2) CHS: the upper and lower portions of Charleston Harbor which contains a deep ship channel as well as a large inlet to the Atlantic Ocean. A few small creeks and sounds are also part of this survey region;
- (3) ACW: includes stretches of the Ashley, Cooper and Wando rivers and selected associated creeks, inland of CHS; and
- (4) CST: the coastal region which includes two transects, an 'on-effort' transect approximately 1km from shore as well as an 'off-effort' route approximately 3km from shore, both stretching from the middle of the Isle of Palms in the east to the eastern end of Kiawah Island to the west.

From 2004–06, boat-based photo-id surveys of bottlenose dolphins were conducted as part of a long-term project to study their abundance and distribution. A complete survey consisted of finishing all transects in each of the four regions in the shortest time possible and under optimal sighting conditions (less than Beaufort Sea State 3). Sixteen

systematic surveys were conducted each year; 12 monthly surveys and an additional seasonal survey in January (winter), April (spring), July (summer) and October (autumn). These seasonal, bi-monthly surveys were the basis for the mark-recapture abundance and survivorship estimates, carried out in close temporal proximity (three weeks) and separated by a minimum of one week to allow for population mixing.

Surveys were conducted from 5–6m centre-console outboard-powered vessels with 3–4 crew members. Surveys followed a designated route at $28\text{--}30\text{ km hr}^{-1}$ until a dolphin or group of dolphins were sighted. An attempt was made to photograph each member of the group, regardless of degree of 'markedness', using a Canon EOS-IDs digital camera equipped with a 100–400mm telephoto lens. A sighting datasheet was completed for each group, defined as all dolphins in close proximity ($<100\text{ m}$) to one another, engaged in similar behaviour and heading in the same direction (Wells *et al.*, 1987). Time, location (via GPS), depth, group size (min, max and best estimate), composition and cohesiveness, environmental conditions, dolphin heading and behaviour were recorded for each group. All dolphin groups encountered while on the designated survey route were regarded as 'on-effort' sightings; whereas, dolphin groups observed while returning along an already completed survey route were labelled as 'off-effort' sightings.

Photo and data analysis

Digital photographs were downloaded and organised by survey date and sighting number. Photographs were then

sorted using *Photoshop* 7.0 to obtain the best left and/or right-side dorsal fin image of each individual from each sighting (Mazzoil *et al.*, 2004). Sorted images were graded for quality using a weighted scale that incorporated five characteristics: focus; contrast; angle; fin visibility/obscurity; and proportion of the frame filled by the fin (Urian *et al.*, 1999). Any photographs not meeting quality criteria were removed from the data set. Only those photographs rated average (Q-2) to excellent (Q-1) quality were included in subsequent analyses.

Q-1 and Q-2 photographs were then matched to the Charleston bottlenose dolphin dorsal fin catalogue via *Finbase*, a customised database constructed using Microsoft *Access* (Adams *et al.*, 2006). All matches were verified by two researchers and catalogued in *Finbase* under a unique numerical code, determined by the most distinctive dorsal fin characteristic. When a fin image was not matched, two researchers independently searched for the fin against the entire catalogue before assigning a new database code. Each sighting of an individual was entered with additional information such as age class and distinctiveness. The extent of dorsal fin markings, in the form of scratches and notches, were used to assign a level of distinctiveness to each individual. Distinctiveness was graded independently of photographic quality. Fins with little to no markings were considered ‘unmarked’. Average fins (D-2; 2 minor or 1 major mark) and very distinctive fins (D-1; obvious major marks) were considered ‘marked’ (Urian *et al.*, 1999).

Capture histories, a record of whether individuals were photographed during each sampling event, were compiled for all ‘marked’ individuals sighted while on-effort during seasonal mark-recapture months (Jan, Apr, Jul and Oct) from 2004–06. In addition, marked individuals photographed during off-effort sightings that occurred within the daily survey region were also included in the capture histories. Capture histories were then exported into *MARK*, a program used to model various parameter estimates from marked animals based on recaptures (Cooch and White, 2006).

Mark-recapture model

Mark-recapture models are defined as either open or closed. Closed population models are conducted over short periods of time and operate under the assumption that the population is constant, that is ‘closed’ to births, deaths, emigration, or immigration. Open models can be conducted over longer periods by allowing for a non-constant population (Pollock *et al.*, 1990). Closed models traditionally used to estimate abundance (e.g. the Lincoln-Petersen method) are further based on the assumptions that: (1) all marks are permanent; (2) being captured does not affect recapture; and (3) all individuals have an equal chance of being captured (Pollock *et al.*, 1990). However, as closure is difficult to achieve in wildlife populations over prolonged periods, survival rates are routinely estimated with open models, (e.g. the Jolly-Seber model) with their own set of assumptions (Pollock *et al.*, 1990). While survival estimates are generally more robust to assumption failures than abundance estimates, assumption violations have the potential to bias either type of estimate (Lebreton *et al.*, 1992). In particular, a violation of ‘equal catchability’, an assumption of both models, can be problematic. Open models somewhat rectify violations of

‘equal catchability’ but are limited in that all emigration from the population is considered permanent (Pollock *et al.*, 1990).

Charleston-area dolphins display a variety of residence patterns (Speakman *et al.*, 2006; Zolman, 2002). Zolman (2002) defined dolphins that were seen year-round in the study area as residents, dolphins that were identified in the same season in multiple years but not during intervening seasons as seasonal residents and dolphins identified in the area in only one season or only two consecutive seasons as transients. Dolphins from all three resident classes have been observed throughout the study area, but seasonal residents and transients are observed more frequently in the coastal region (Speakman *et al.*, 2006). Seasonal residents are commonly observed feeding behind working shrimp boats along the Charleston coast during peak shrimp season from June to November. These dolphins are often sighted in Charleston Harbor following returning shrimp boats and likely represent individuals who reside beyond the study area making seasonal forays into Charleston waters. Such movements through the study area would obviously test the assumption of ‘equal catchability’ if the recapture period extended across seasons.

Due to these considerations, Pollock’s robust design model (Pollock, 1982) was applied to three years of mark-recapture data to estimate abundance and survival rates. This model follows a set of assumptions derived from both open and closed population models to estimate parameters. These assumptions include: (1) all marks are unique and permanent; (2) survival is equal among all individuals between primary sampling periods; (3) each individual’s probability of capture and survival is independent of all others; (4) the population is closed within primary sampling periods; and (5) all emigration between primary sampling periods is temporary (Kendall *et al.*, 1995). By incorporating both open and closed population models, the robust model allows for the effects of temporary emigration on the population, thus making it less sensitive to violations of ‘equal catchability’ (Pollock, 1982). Advantages of the robust model include better precision and less biased results due to its ability to account for temporary emigration. The surveys produced data for 12 primary sampling periods (Jan, Apr, Jul, Oct for 2004–06), each containing two, secondary sampling occasions. The robust model enabled abundance estimates for each primary session (with closed population models) and survival estimates for intervals between primary sessions (using an open population model) (Pollock *et al.*, 1990).

Calculating abundance and survival estimates

The master, or ‘complete’ data set used in this study includes marked individuals identified during all sightings within the survey area from 2004–2006. Data were analysed within *MARK* via the robust design model with closed captures. Parameters were adjusted within the Parameter Index Matrix (PIM) to represent various closed population models, such as M_{01} , M_{11} and M_{10} . M_{01} , the simplest model, assumes no variation in capture probabilities among animals or sampling occasions (Seber, 1992). M_{11} assumes each animal has a constant capture probability on any sampling occasion but probabilities of capture can vary from one occasion to the

next (Seber, 1992). The behavioural response model, M_b , incorporates change in capture probability as a result of previous capture (i.e. trap-happy or trap-shy) (Seber, 1992). Furthermore, each model was constrained to test for variations in emigration patterns (e.g. random or Markovian emigration) (Kendall *et al.*, 1997). Random emigration assumes that an individual emigrates out of the study area for just one sampling occasion and then always comes back, but can emigrate again randomly (Kendall *et al.*, 1997). Markovian movement assumes individuals that have temporarily emigrated from the study area at time t are more likely to be out of the study area at time $t + 1$ than those that remained in the study area at time t (i.e. animals ‘remember’ they are out of the area) (Kendall *et al.*, 1997). Finally, survival was held constant among all models as historical stranding records from the area failed to show an effect of season on the number of non-neonate stranded dolphins (McFee *et al.*, 2006). The best fitting model was selected based on the variance inflation factor (\hat{c}), model deviance and Akaike’s information criterion corrected for small sample size (AICc), which is an information criteria designed to maximise model fit without compromising precision (Burnham and Anderson, 2002).

Seasonal abundance estimates derived from *MARK* were compared to seasonal estimates calculated using a simple Lincoln-Petersen model following closed population assumptions (Pollock *et al.*, 1990). Additionally, for comparison, monthly counts of marked individuals were calculated. All on-effort sightings of distinctively marked individuals were used and monthly counts for single-sighted marked individuals were calculated to examine when permanent immigration/emigration might be occurring. Select data sets, such as those excluding sightings of all shrimp boat-associated individuals (‘shrimp boat delimited’) and of all individuals encountered during CST surveys (‘CST delimited’), were also constructed and analysed. The ‘shrimp boat delimited’ data set was constructed to examine the effect that seasonal resident and transient dolphins, which are frequently associated with shrimp boats, might have on abundance estimates. Removing dolphins sighted along the CST, in combination with those associated with shrimp boats, allowed for estuarine abundance estimates.

MARK-derived estimates represent only the distinctively ‘marked’ portion of the Charleston dolphin population. To adjust this estimate of ‘marked’ abundance to estimate total abundance (‘unmarked’ plus ‘marked’ dolphins), the ‘marked’ estimates were divided by the ‘marked’ proportion of the population for each primary session. To calculate this proportion, all on-effort sightings were compiled for each primary session from 2004–06 in which all dolphins in the group, regardless of distinctiveness level, were photographed. Variance and confidence intervals for each seasonal total abundance estimate were calculated using the delta method (Wilson *et al.*, 1999).

Annual survival rates (ASR) for the ‘marked’ portion of the population were estimated from the product of the seasonal survival rates (i.e. $S_{Jan} \times S_{Apr} \times S_{Jul} \times S_{Oct} = S^4$). The delta method (Wilson *et al.*, 1999) was again used to calculate the variance and confidence intervals for the ASR. Dorsal fin markings in small cetaceans are cumulative (Würsig and Jefferson, 1990) and consequently, very young

dolphins have a lower likelihood of having distinctive fins. Therefore, young-of-the-year (YOY) survivorship rates were estimated separately from the rest of the population. This was accomplished by tracking the sighting records of calves born to distinctive females from 2004 to 2006. Calves were classified as deceased if the mother was encountered either with the carcass of the calf or without the calf on three or more consecutive sightings. Age was approximated in months for each calf using the month of initial and final sighting as endpoints for the age interval. Birth was assumed to have occurred in the same month as each calf’s initial sighting; therefore any individual thought to be an older calf (i.e. those lacking fetal folds) (Urian and Wells, 1996) was excluded from YOY survivorship estimation. For those individuals not classified as dead prior to the conclusion of the study, final sightings were treated as right censored observations; thereby allowing for the incorporation of all available lifetime data into the survival analysis although only a fraction of exact lifetimes were known. Due to the censoring of these data, the YOY survivorship rate was derived utilising a Kaplan-Meier product-limit estimator,

$$\hat{S}(t) = \prod_{i \leq t} [1 - d_i / Y_i], \quad (1)$$

where t_i is time, d_i is the number of deaths at time t and Y_i is the number of individuals in the sample at time t (Klein and Moeschberger, 1997).

RESULTS

Forty seven surveys from January 2004 through December 2006 were completed. Only one survey (CST June 2004) was incomplete. During the three year project a total of 1,423hrs were spent on the water ($n = 562$ hrs in contact with dolphins), 9,217km were surveyed on-effort, 96,153 photographs were taken and 2,272 (1,961 on-effort) dolphin groups were encountered. Within on-effort groups, 856 distinctively marked individuals were identified. The calculated marked proportion of individuals sighted varied across seasons and ranged from 60% to 73%. A total of 556 (65%) marked individuals were sighted more than once (Fig. 2).

An influx of transient dolphins was observed in the autumn months of both 2005 and 2006 as indicated by an increase in the number of individuals not previously sighted

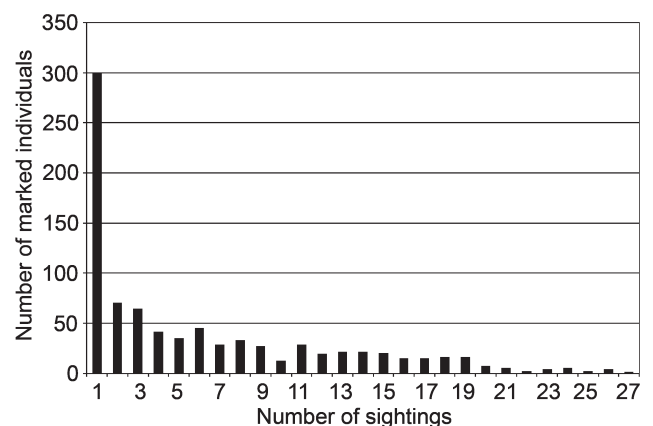


Fig. 2. Sighting frequency of marked individual dolphins within the Charleston study area from 2004–06.

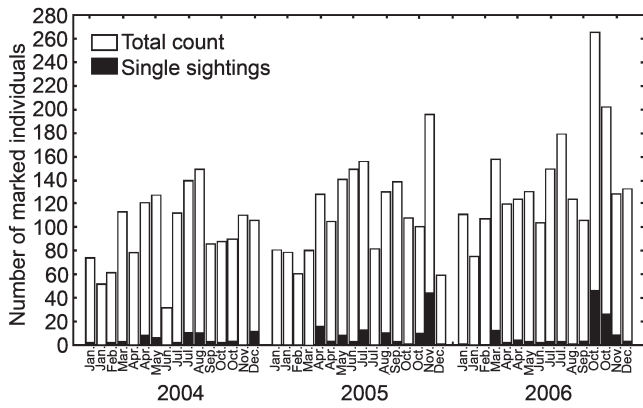


Fig. 3. Total counts and number of single-sighted marked dolphins per month within the Charleston study area from 2004–06.

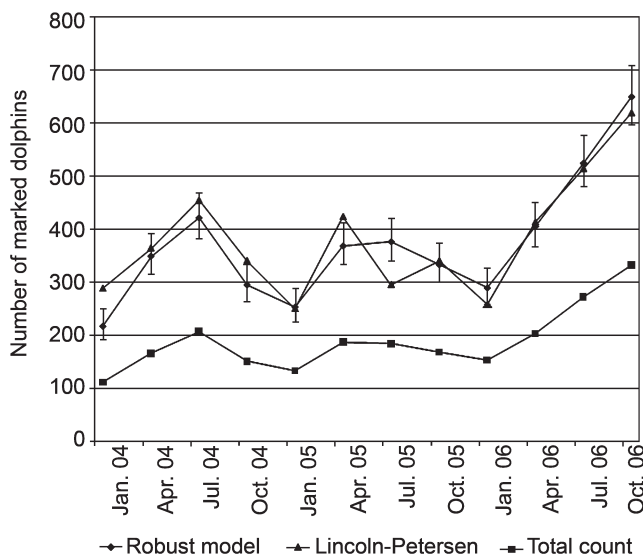


Fig. 4. Seasonal abundance of marked dolphins in the Charleston study area estimates from Pollock’s robust design model, Lincoln-Petersen model and total counts from 2004–06.

(Fig. 3). Additionally, a near doubling of previous total marked dolphin counts was observed in the summer and autumn of 2006 (Fig. 4).

The M_0 model with Markovian movement demonstrated the lowest AICc and variance inflation factor (\hat{c}), but still suggested a poor model fit and over dispersion (Table 1). The variance inflation factor, the degree to which an individual variable is correlated with other individual variables in the model (O’Brien, 2007), equal to one generally represents a good fitting model. The observed \hat{c} value of 7.86 reflects

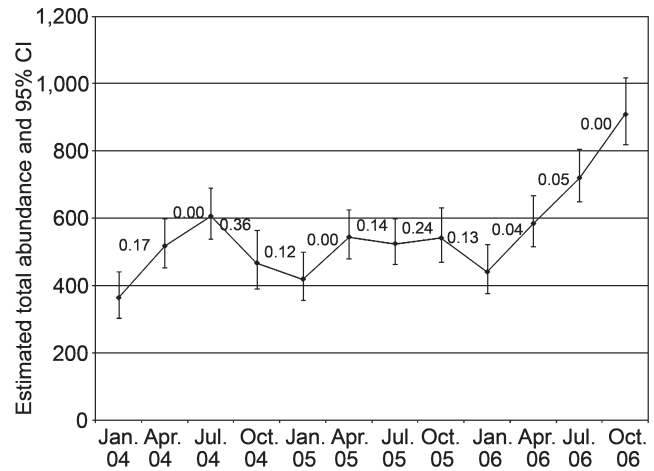


Fig. 5. Seasonal total (marked and unmarked) abundance estimates with 95% confidence intervals and emigration parameters for the Charleston study area from 2004–06.

over dispersion likely resulting from a violation of one or more model assumptions (Anderson *et al.*, 1994).

Abundance estimates

Estimates derived from both the Lincoln-Petersen and robust design (M_0 , Markovian) models followed the same general seasonal trend with the greatest abundance estimates seen in the summer and the lowest abundance estimates in the winter (Fig. 4). The highest abundance estimates of marked individuals resulting from the robust design model occurred in autumn 2006 ($N = 649$, 95% CI = 598–709) while the lowest were found in winter 2004 ($N = 217$, 95% CI = 192–250). These corresponded to overall abundance estimates (after adjustment for seasonal unmarked proportion) of 910 (95% CI = 819–1018) and 364 (95% CI = 305–442) in autumn 2006 and winter 2004, respectively (Fig. 5).

Excluding 2006, estimated emigration parameters (Fig. 5) were also suggestive of an efflux of dolphins from the study area between summer and autumn. The highest probabilities of emigration were for the periods between July and October 2004 ($\hat{\gamma} = 0.36$) and July and October 2005 ($\hat{\gamma} = 0.24$).

The ‘shrimp boat delimited’ data set resulted in lower summer 2004 estimates (‘complete’ data set $N = 421$; ‘shrimp boat delimited’ data set $N = 363$) while there was very little difference observed in either 2005 (‘complete’ data set $N = 376$; ‘shrimp boat delimited’ data set $N = 378$) or 2006 summer (‘complete’ data set $N = 524$; ‘shrimp boat delimited’ data set $N = 513$) estimates. The ‘CST and shrimp boat delimited’ data set, representing the estuarine portion of

Table 1

MARK program results summarising AICc, number of parameters, deviance and variance inflation factor (\hat{c}) from closed population models utilising Pollock’s robust design.

Model	AICc	Delta AICc	No. of parameters	Deviance	\hat{c}
M_0 (Markovian)	-9,715.41	0	35	3,214.81	7.86
M_b (Markovian)	-9,713.97	1.44	36	3,214.19	7.88
M_1 (Markovian)	-9,706.76	8.64	46	3,200.79	8.04
M_b (Random)	-9,669.71	45.70	26	3,278.90	7.84
M_0 (Random)	-9,659.75	55.66	25	3,290.90	7.85
M_1 (Random)	-9,645.85	69.56	36	3,282.31	8.04

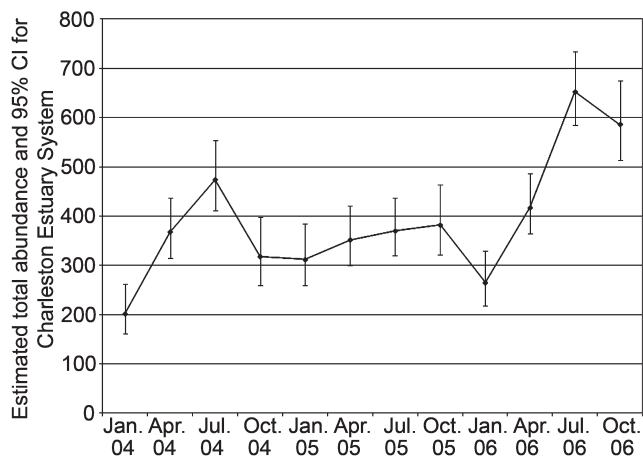


Fig. 6. Seasonal total (marked and unmarked) abundance estimates with 95% confidence intervals for the Charleston Estuarine System (excludes CST) from 2004–06.

the study area, resulted in total abundance estimates ranging from 202 (95% CI = 162–262) to 652 (95% CI = 585–734) (Fig. 6).

Survival estimates

The M_0 model with Markovian movement provided a seasonal survival rate of 0.987 (SE = 0.009, 95% CI = 0.949–0.997) resulting in an ASR of 0.951 (SE = 0.035, 95% CI = 0.882–1.00). For YOY survival, a total of 62 calves were sighted with distinctive mothers during monthly photo-ID surveys from 2004–06 and were included in a survival analysis. By December 2006, 17 individuals were considered dead, 13 (76%) of which were estimated to have died within three months of birth. Using the Kaplan-Meier product-limit estimator, a YOY survival rate of 0.754 was estimated (SE = 0.059, 95% CI = 0.647–0.878).

DISCUSSION

Assessment of mark-recapture assumptions

The present analysis of abundance and survivorship is contingent upon a set of assumptions derived from both open and closed population models (see the 'Mark-recapture model' section of 'Methods'). Violations of these assumptions have the potential to bias parameter estimates and should be considered.

A violation of assumption 1 (all marks are unique and permanent) is unlikely. The major distinguishing characteristics used to identify bottlenose dolphins (marks from conspecifics, shark bites, dorsal fin mutilations and tears, collision injuries, etc.) are generally persistent and can last throughout an individual's lifetime (Lockyer and Morris, 1990; Würsig and Jefferson, 1990). Implementation of the fin and photo grading processes helped mitigate the possibility of fin misidentification. Misidentification due to the appearance of new markings altering or obstructing previous marks is more likely. However, with the exception of total fin mutilation/amputation, itself an infrequent phenomenon, the classification criteria requiring that 'marked' fins exhibit at least two distinguishing fin characteristics reduces the chance of this occurring. Additionally, the monthly frequency in which surveys were

conducted further decreases the likelihood of altered fin misidentifications.

The second assumption (equal survival among all individuals between primary sampling periods) may potentially be violated with the inclusion of all age classes in the analysis. While long-lived species generally exhibit strong age-specific survivorship (Pearl and Miner, 1935), the period between primary sampling occasions is relatively short (three months) compared to a dolphin's overall lifetime; therefore, it is reasonable to assume survival rates for all individuals are equal over this time period. Furthermore, the individuals with the highest likely mortality rates, young-of-the-year (Stolen and Barlow, 2003), were generally excluded in the mark-recapture analysis due to their inherent lack of distinctive markings (Würsig and Jefferson, 1990).

Given that most young-of-the-year were excluded from the survivorship analysis, a violation of assumption 3 (independence of capture and survival probabilities between individuals) is also unlikely. Bottlenose dolphins live in a social society in which mother/calf associations are normally maintained throughout the first few years of a calf's lifetime (Wells *et al.*, 1987). While unmarked calves are generally only identified by association with their mother, sample independence can be upheld with the removal of these individuals from the analysis. Although other associations also form within dolphin groups (e.g. subadult and nursery groups), the fluid nature of these associations reduces the likelihood of violating this assumption (Wells *et al.*, 1987).

As for previous photo-id efforts in this area (Speakman *et al.*, 2006; Zolman, 2002), this study found evidence of transient individuals which could violate assumption 4 (population closure within primary sampling periods). Specifically, a significant influx of dolphins during summer and autumn 2006 was suggested by the unusually large total counts during this period, combined with a high number of single-sighted individuals (Fig. 3). The presence of transient individuals which move out of the study within a single primary session could result in an upward bias of abundance estimates and for this reason, the abundance estimates for the latter part of 2006 should be viewed with caution.

Similarly, the presence of transient individuals may violate assumption 5 (all emigration between primary sampling periods is temporary). Approximately 300 marked individuals were sighted only once representing individuals that either died or permanently emigrated (Fig. 2). Given that the robust model only accounts for temporary emigration, it is unable to differentiate between permanent emigration and death, resulting in a downward bias of the survival estimate.

Abundance estimates

Total abundance estimates, including both marked and unmarked dolphins, varied considerably among primary survey sessions, ranging from 364 (95% CI = 305–442) in January 2004 to 910 (95% CI = 819–1018) in October 2006 (Fig. 5). A consistent trend of low winter estimates, increasing in the spring, is evident for all three years. Excluding 2005, estimates continue to increase through summer. All three autumn estimates varied greatly, dropping off from summer 2004, holding steady with spring and summer 2005 and continuing to increase in 2006.

Although estimates exhibited a great deal of seasonal and annual variability, differences were detected between summer and winter in all three years (evidenced by a lack of overlap between 95% CIs; Fig. 5). The three winter estimates represented the lowest seasonal estimates across all three years. The data suggest that certain dolphins move into the Charleston area throughout spring and summer before emigrating beyond the study area for the winter, supporting earlier findings of short-term or seasonal resident dolphins around Charleston (Speakman *et al.*, 2006). High sighting frequencies (Fig. 2) and year-round presence suggest that other dolphins remain in the Charleston study area throughout the year, a finding first reported by Zolman (2002). Similar patterns of seasonal variability in abundance have been noted for bottlenose dolphin populations in Florida (Weigle, 1990) and Texas (Bräger, 1993; Fertl, 1994).

The observed low abundance in winter could be due to a shift in prey distribution during colder months. Both Irvine *et al.* (1981) and Fazioli *et al.* (2006) noted a shift in distribution of ‘inshore’ dolphins toward passes leading to the Gulf of Mexico near Sarasota, Florida, during the winter months perhaps in association with the migration of spawning mullet. Young and Phillips (2002) found a decline in prey availability in a South Carolina estuary during the winter months, resulting in a shift in creek utilisation patterns of the dolphins. It is hypothesised that dolphins move outside the study area during winter months, either into the upper reaches of the rivers and creeks or offshore, where greater densities of prey may be located (Pate, 2008).

Conversely, the observed differences could be due to increases in dolphin numbers during summer. Summer abundance estimates of marked individuals were highest in both 2004 and 2005 and were even higher in 2006 (only to be surpassed by the following autumn estimate; Fig. 4). Additional dolphins might utilise the Charleston study area during the summer for increased reproductive activity (Thayer *et al.*, 2003). This could cause an increase in receptive females and also males seeking mating opportunities. Increased shrimp trawling during summer could also lead to more dolphins. In Galveston, Texas, where dolphins have also been documented interacting with shrimp boats, Fertl (1994) reported an increase in recognisable dolphins in late summer. Dolphins were often observed within the CHS region following shrimp boats in from the coast, actively feeding on discarded bycatch. To assess the impact of trawling-related changes in dolphin abundance, abundance estimates were re-calculated using the ‘shrimp boat delimited’ data set. Although this resulted in a decline in the summer 2004 estimate (‘complete’ data set’ N = 421; ‘shrimp boat delimited’ data set N = 363), there was very little difference observed in either 2005 or 2006 summer estimates.

The largest variability in abundance occurred in 2006, where estimates were highest for each season and steadily increased from winter through to autumn. This influx, which is inconsistent with the patterns seen in the two previous years, suggests that stock movements and/or migration may occur sporadically and not necessarily predictably across years. No unusual circumstances (e.g. extreme weather patterns or water temperatures) could be found that might

have prompted the additional movement of dolphins into the study area in 2006. The pattern of single-sighted individuals, along with estimated emigration parameters, provides insight into the inconsistent trend of abundance. In 2004 and 2005, the highest probabilities of emigration occurred between July and October (Fig. 5), consistent with a decrease in abundance. This suggests an efflux of seasonal residents from the study area between summer and autumn. In these same years, the autumn influx of single-sighted individuals (transients) occurred later in the autumn (November 2005) or winter (December 2005) (see Fig. 3), after the October abundance estimate. On the other hand, the peak in single-sighted individuals occurred earlier (October) in 2006 while emigration was low (0.00), suggesting that transients immigrated into the study area earlier in 2006. At the same time, seasonal residents had yet to emigrate as in the previous two years, hence the extremely high summer and autumn estimates in 2006.

There is some evidence for extralimital movements by a number of Charleston transient dolphins. Seven individuals have been matched to sites ranging from Jacksonville, FL to Wilmington, NC (K. Urian, pers. comm.) through the Mid-Atlantic Bottlenose Dolphin Catalog (MABDC) (Urian *et al.*, 1999). The MABDC was established by NMFS in 1997 as a cooperative program that includes images and data from multiple photo-id researchers along the mid-Atlantic in order to clarify stock structure of coastal bottlenose dolphins along the western North Atlantic (Urian *et al.*, 1999). These seven matches, all sighted during coastal surveys, were made as part of the curator’s selection process of the Charleston catalogue; at present, a more rigorous matching effort has not been undertaken. Of the seven matches, three were sighted between 2004 and 2006; two of these were off-effort coastal sightings and thus, not included in the survivorship or abundance analyses, with the lone on-effort dolphin sighted off Jacksonville, FL in 1997. Future work should involve additional matching effort to the MABDC in order to determine if more Charleston dolphins have been sighted in other areas along the Atlantic coast and if there is a seasonal migratory trend.

Additionally, these findings suggest a need for extending our survey efforts over the next several years to assess whether the observed influx was temporary or indicative of a permanent movement or pattern of movement. They also suggest that caution should be used in employing abundance estimates or observed patterns of movement obtained from studies that have been conducted over relatively short time periods. Such studies may be influenced by unusual events, such as we observed in 2006, without obvious cause.

The accuracy of abundance estimates can be determined by examining capture probabilities (Otis *et al.*, 1978, e.g. for this study, capture probability is the likelihood that a dolphin is photographed). For example, Otis *et al.* (1978) found that capture probabilities less than 0.10 resulted in significant bias of abundance estimates whereas when capture probabilities were greater than 0.30, abundance estimates were reliable and useful, with good confidence interval coverage. Using these criteria, the average capture probability for our three year study was 0.31, within the range of reliable values.

Survival estimates

By reporting the survival estimates in conjunction with abundance estimates it is possible to better evaluate potential biases associated with the survival estimate. Although Speakman *et al.* (2006) previously identified the presence of seasonal residents and transients within the study area, the extent to which these individuals occur is unknown. The abundance estimates presented in this study exhibit seasonal differences with significantly higher estimates in the summer than in the winter every year (Fig. 4). This pattern, in conjunction with the relatively high temporary emigration rates, γ^* , observed between the summer and autumn of 2004 and 2005 ($\gamma^* = 0.36$ and $\gamma^* = 0.24$ respectively; Fig. 5), suggests an influx of seasonal residents throughout the summer months. The temporary, seasonal movement patterns exhibited by these individuals are accounted for within the model by the temporary emigration parameter, γ^* ; however, permanent movements by individuals captured once within the study area (i.e. transients) may alter the temporary emigration parameter, thus affecting survival estimates. Accordingly, the lack of precision and high variability in the temporary emigration estimates (Table 2) likely reflects the repeated autumnal influx of single-sighted individuals observed over all three years (Fig. 3), a movement pattern indicative of transient individuals. Because the robust model is unable to differentiate between permanent emigration and death, such imprecision and variability in the temporary emigration estimates suggests the survival estimate may also be biased.

Temporary emigration was modelled by incorporating Markovian and random movement patterns into each model. For each model (M_o , M_t and M_b), the data provided greater support for Markovian movement (Table 1). Markovian movements, where individuals that temporarily emigrate from the study area ‘remember’ they are out of the area (Kendall *et al.*, 1997), are biologically reasonable for seasonal migration.

Transient individuals, i.e. permanent emigrants, may have influenced the estimation of survival rates, resulting in downward bias (ASR = 0.951, SE = 0.030, 95% CI = 0.891–1.00). However, this rate is comparable to survival rates reported for other *Tursiops* populations within the southeastern US (Fig. 7, and see Stolen and Barlow, 2003; Wells and Scott, 1990). Potential biases associated with the

Table 2

Temporary emigration parameter estimates for periods between each consecutive primary sampling occasion derived from the robust design (M_o , Markovian) model in *MARK*.

Parameter	Estimate	Standard error	95% CI
γ^* Jan. 04–Apr. 04	0.168	0.090	0.054–0.417
γ^* Apr. 04–Jul. 04	0.000	0.000	N/A
γ^* Jul. 04–Oct. 04	0.359	0.055	0.260–0.472
γ^* Oct. 04–Jan. 05	0.121	0.061	0.043–0.297
γ^* Jan. 05–Apr. 05	0.000	0.000	N/A
γ^* Apr. 05–Jul. 05	0.141	0.050	0.068–0.269
γ^* Jul. 05–Oct. 05	0.235	0.045	0.157–0.334
γ^* Oct. 05–Jan. 06	0.132	0.055	0.056–0.281
γ^* Jan. 06–Apr. 06	0.039	0.059	0.002–0.471
γ^* Apr. 06–Jul. 06	0.047	0.040	0.008–0.224
γ^* Jul. 06–Oct. 06	0.00	0.00	N/A

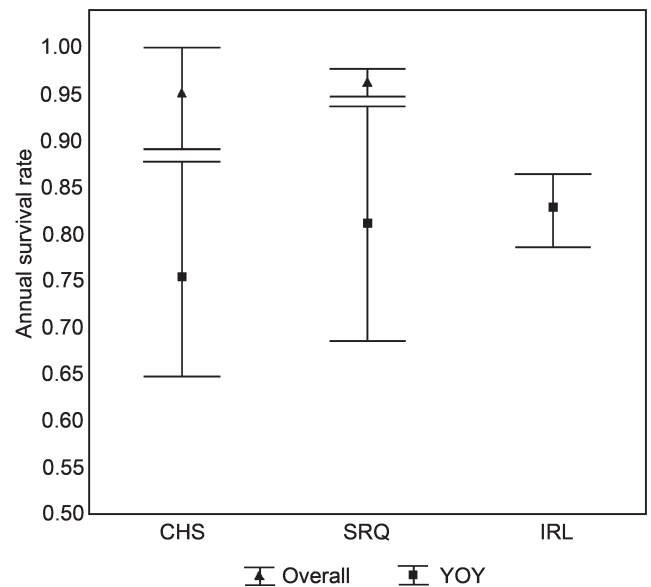


Fig. 7. Survival estimates for marked individuals and the young-of-the-year age class derived for various bottlenose dolphin communities in the southeastern US: Sarasota Bay, FL^a (SRQ), the Indian River Lagoon, FL^b (IRL) and Charleston, SC (CHS). Error bars represent 95% CI of the estimated mean.

YOY survival estimate must also be considered. Until the time of weaning (~2–3 years) calves entirely depend on their mothers (Wells *et al.*, 1987). Consequently, if a mother dies within her calf’s first year of life there is little chance the dependent calf will survive. Calves included in the analysis were identified by their associations with distinctive mothers; if a mother disappeared it was not possible to determine the fate of her calf. This has the potential to bias survival estimates if a calf dies subsequent to its mother’s final sighting. Furthermore, the estimate does not reflect the mortality of neonates that died before initial capture (i.e. before being observed). Therefore, the YOY survival rate of 0.754 (SE = 0.059, 95% CI = 0.647–0.878) should be regarded as a minimum level of mortality for this population. The estimate obtained in this study is lower than that reported for YOY in other *Tursiops* populations (Fig. 7, and see Stolen and Barlow, 2003; Wells and Scott, 1990). This difference may be due to environmental variations between the study sites including geography (Stolen and Barlow, 2003; Wells and Scott, 1990) and contaminant levels (Fair *et al.*, 2007; Hansen *et al.*, 2004; Schwacke *et al.*, 2002; Wells *et al.*, 2005); however, due to the high degree of variance associated with our estimate, a statistically significant difference between sites could not be detected.

Management implications

An important goal of this study was to establish baseline abundance estimates for bottlenose dolphins inhabiting the Charleston study area and understand seasonal movements through the area. Ideally, these estimates would be used to resolve some of the complexities of bottlenose dolphin stock structure along the coast of the WNA by providing a more comprehensive definition for the local stock. Recently,

^a Wells and Scott (1990).

^b Data reported by Stolen and Barlow (2003).

scientists from the NMFS Southeast Fisheries Science Center began drafting Stock Assessment Reviews for previously unaddressed estuarine areas along the USA Atlantic Coast (Waring *et al.*, 2009; L. Hansen pers. comm.). Based on research conducted over the past 14 years on bottlenose dolphins around Charleston, a new ‘Charleston Estuarine System Stock’ was defined and boundaries for this new stock include the study area reported here. The boundaries have been defined as the inshore, estuarine subareas to the north and south of Charleston Harbor, excluding the coast. Thus, the analysis herein provides an abundance estimate for this newly proposed estuarine stock of dolphins. Estimates were calculated from the ‘CST and shrimp boat delimited’ data set using the robust design model (M_0 , Markovian) in MARK and adjusted for seasonal unmarked proportions (ranging from 0.28 to 0.44). The Delta method was used to calculate variance and confidence intervals (Wilson *et al.*, 1999, and see Fig. 6). By excluding coastal and shrimp boat sightings, the number of single-sighted dolphins was reduced by more than half (300 to 112), thus better representing the more resident, estuarine segment of the population. Total abundance estimates ranged from 202 (95% CI = 162–262) in January 2004 to 652 (95% CI = 585–734) in July 2006. Estuarine abundance exhibited trends similar to the ‘complete’ data set with significantly higher estimates in summer than in winter as well as the highest estimates for each season in 2006. The autumn 2006 estimate was noticeably smaller (from 910 to 586) after removing the single-sighted dolphins associated with the CST region.

Read *et al.* (2003) conducted a similar mark-recapture study of bottlenose dolphins in the bays, sounds and estuaries of North Carolina during July 2000. Their study resulted in a summer abundance estimate of 1,033 dolphins which, to date, is the only estimate for estuarine dolphins in the most recent NMFS stock assessment for the WNA population (Waring *et al.*, 2009). The July estimates from 2004 and 2005 (474 and 370, respectively), presented herein, appear to best represent summer abundance, while January estimates from 2005 and 2006 (312 and 265, respectively) provide the most accurate winter abundance estimate for the Charleston estuarine population.

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