Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA

B.C. BALMER[+,*], R.S. WELLS[*], S.M. NOWACEK[*], D.P. NOWACEK[¥], L.H. SCHWACKE[€], W.A. MCLELLAN[+], F.S. SCHARF[+], T.K. ROWLES[Ω], L.J. HANSEN[£], T.R. SPRADLIN[Ω] AND D.A. PABST[+]

Contact e-mail: bbalmer@mote.org

ABSTRACT

Three unusual mortalities events involving bottlenose dolphins (*Tursiops truncatus* Montagu 1821) occurred along Florida's northern Gulf of Mexico coast between 1999 and 2006. The causes of these events, in which over 300 bottlenose dolphins are known to have died, are still under investigation. The impact of these mortality events cannot be fully evaluated, because little prior information on bottlenose dolphin abundance and distribution patterns exist in this region. Thus, the goals of this study were to estimate seasonal abundance, develop site-fidelity indices, and describe distribution patterns of bottlenose dolphins in St. Joseph Bay, Gulf County, Florida, USA. This study site was chosen because it was impacted by all three unusual mortality events and was the geographic focus of the 2004 event. Mark-recapture photo-identification surveys were conducted across multiple seasons from February 2005 through July 2007. Site-fidelity indices were calculated for each identifiable dolphin based upon all photo-ID efforts undertaken in the area. Distribution patterns were investigated by short-term (12-94 days) radio-tracking of tagged individuals across seasons (April-July, n=9; July-October, n=15). Mark-recapture closed and robust abundance estimates, as well as site-fidelity indices suggest that St. Joseph Bay supports a resident community of 78-152 bottlenose dolphins. During spring and autumn, this region experiences an influx of dolphins, as demonstrated by closed and robust abundance estimates of 313-410 and 237-340, respectively. These results are supported by the distribution patterns of radio-tagged individuals. Individuals tagged in summer tended to stay within or near St. Joseph Bay, whereas two individuals tagged in spring ranged more than 40km from the study site. This study provides the first detailed examination of bottlenose dolphin abundance and distribution patterns for this region of the northern Gulf coast of Florida. These results suggest that unusual mortality events probably had, and will in the future have, seasonally variable effects on bottlenose dolphins in St. Joseph Bay. Future mortality events that occur during the summer and winter in St. Joseph Bay may predominantly affect resident individuals, while those that occur during the spring and autumn will probably affect both residents and seasonal visitors.

KEYWORDS: BOTTLENOSE DOLPHIN; ABUNDANCE ESTIMATE; MARK-RECAPTURE; SITE- FIDELITY; PHOTO-ID; RADIO-TAGGING; NORTH AMERICA

INTRODUCTION

Our ability to assess the impacts of natural and anthropogenic catastrophic events on populations of bottlenose dolphins, *Tursiops truncatus* Montagu (1821), suffers from a general lack of baseline information on stock structure and abundance in many areas (McLellan *et al*., 2002; Wells *et al*., 2004). For example, between 1999 and 2006 along Florida's northern Gulf of Mexico coast, bottlenose dolphins experienced three large scale mortality events, resulting in over 300 bottlenose dolphin deaths (NMFS, 2004; Waring *et al*., 2007). These events were defined as 'Unusual Mortality Events' (UMEs) because of their distinct dissimilarity to normal stranding patterns in this region (1972 Marine Mammal Protection Act + 1992 Amendments). Although the causes of these events are still under investigation, they may have been spatially and temporally correlated with blooms of *Karenia brevis*, the dinoflagellate known to cause red tide harmful algal blooms (HABS) in Florida (NMFS, 2004). However, the impact of these UMEs cannot be fully evaluated because the structure and size of bottlenose dolphin stocks in the northern Gulf of Mexico are not well understood (Waring *et al*., 2007).

In the United States, all marine mammals are protected under the Marine Mammal Protection Act (MMPA), which is jointly administered by the National Marine Fisheries Service under the National Oceanic and Atmospheric Administration (NOAA Fisheries Service), and the United States Fish and Wildlife Service. Specifically for bottlenose dolphins, stock assessments are conducted and conservation plans are implemented as necessary by NOAA Fisheries Service. Currently, stocks of bottlenose dolphins that inhabit each bay and estuary in the northern Gulf region are defined and managed as separate estuarine communities, largely based on geographical features rather than on empirical data on ranging patterns or genetics (Waring *et al*., 2007). A community is a group of resident animals that share home ranges, display similar genetic features, and interact more frequently with each other than with dolphins in adjacent waters (Wells *et al*., 1987). In addition, NOAA identifies eastern, northern, and western stocks of coastal bottlenose dolphins within the Gulf of Mexico (Waring *et al*., 2007). The coastal waters are defined as shoreline and bay boundaries to the 20m isobath (Waring *et al*., 2007). Thus, there is potential geographic overlap of coastal and estuarine bottlenose dolphins.

[+] *Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC 28403, USA.*
[*] *Chicago Zoological Society, c/o Mote Marine Laboratory, Sarasota, FL 34236, USA.*
[¥] *Department of Oceanography, Florida State University, Tallahassee, FL 32306, USA.*
[€] *NOAA Ocean Service, Charleston, SC 29412, USA.*
[Ω] *NOAA/National Marine Fisheries Service, Silver Spring, MD 20901, USA.*
[£] *NOAA Fisheries Service, Beaufort, NC 28516, USA.*

Long-term resident communities of bottlenose dolphins, as well as dolphin groups that display seasonal movements have been identified along the Texas coastline (Bräger, 1993; Fertl, 1994; Gruber, 1981; Irwin and Würsig, 2004; Lynn and Würsig, 2002; Maze and Würsig, 1999; Shane, 1977; Weller, 1998) and within Mississippi Sound (Hubard *et al*., 2004). Relatively stable, long-term resident communities of bottlenose dolphins have also been identified in Sarasota Bay, Florida (Irvine *et al*., 1981; Wells, 1986; Wells *et al*., 1987) and in the adjacent large estuaries of Charlotte Harbor (Wells *et al*., 1997) and Tampa Bay (Wells, 1986). Long range movements of coastal bottlenose dolphins have been observed in the 'western' Gulf stock, along the coast of Texas (Beier, 2001; Lynn and Würsig, 2002). Both 'eastern' coastal and estuarine bottlenose dolphin stocks have been identified within the coastal waters of Tampa Bay, Sarasota Bay, and Charlotte Harbour (Fazioli *et al*., 2006). Currently, community structure and seasonal movements of bottlenose dolphins along the northern Gulf coast of Florida are unknown.

Identifying stocks, estimating the number of individuals belonging to those stocks, and determining individuals' distribution patterns are necessary steps for establishing effective management plans (Macdonald *et al*., 1979; Taylor and Gerrodette, 1993; Westgate and Read, 1998). Systematic surveys and mark-recapture methods utilising photographically-identified individuals have yielded insights into patterns of bottlenose dolphin abundance and site-fidelity in other geographic regions (e.g. Barco *et al*., 1999; Maze and Würsig, 1999; Read *et al*., 2003; Seber, 1982; Shane, 1980; 1990a; 1990b; Torres *et al*., 2005; Wells, 1986; Wells, 1994; Williams *et al*., 1993; Wilson *et al*., 1999; Würsig and Würsig, 1977). Radio-tracking of individuals has provided insight into cetacean short-term distribution patterns (e.g. Evans, 1971; Perrin, 1975; Leatherwood and Evans, 1979; Norris and Dohl, 1980; Irvine *et al*. 1981; Read and Gaskin, 1985; Watkins *et al*. 1999).

The goals of this study were to utilise mark-recapture photo-identification (ID) surveys and radio-tracking of individuals to provide baseline data on the abundance and distribution patterns of bottlenose dolphins in St. Joseph Bay, Gulf County, Florida, USA. This study site was chosen because it was impacted by all three UMEs, and was the geographic focus of the 2004 mortality event. These techniques were used to: (1) provide accurate, seasonal estimates of bottlenose dolphin abundance in the St. Joseph Bay region; (2) identify the level of site-fidelity expressed by individual animals on a seasonal and interannual scale; and (3) determine distribution patterns of individuals across seasons. Photo-ID surveys were conducted over three years to generate seasonal abundance estimates. Multiple, independent photo-ID surveys of dolphins in the St. Joseph Bay region were used to calculate site-fidelity indices. Radio-tracking of individual bottlenose dolphins near St. Joseph Bay was used to identify distribution patterns across two seasonal transitions.

METHODS

Mark-recapture photo-identification surveys

The mark-recapture survey area included the Gulf of Mexico waters from Cape San Blas northwest to and including Crooked Island Sound and St. Joseph Bay (Fig. 1). The survey design used both line and contour transects to cover the entire region (Fig. 1). St. Joseph Bay was divided into 18 east-west line transects, spaced 1km apart. In regions where water depth was less than 1m (i.e. southern St. Joseph Bay and Crooked Island Sound), contour transects along the 1m isobath were used to survey the area. Contour transects are line transects that follow a particular geographic feature such as bathymetry or coastline. Contour transects that followed the coastline were used to cover the Gulf regions, extending from Cape San Blas northwest to the entrance of Crooked Island Sound, at distances of 0.5km and 1.5km from shore. Transects were followed with the assistance of a GPS unit.

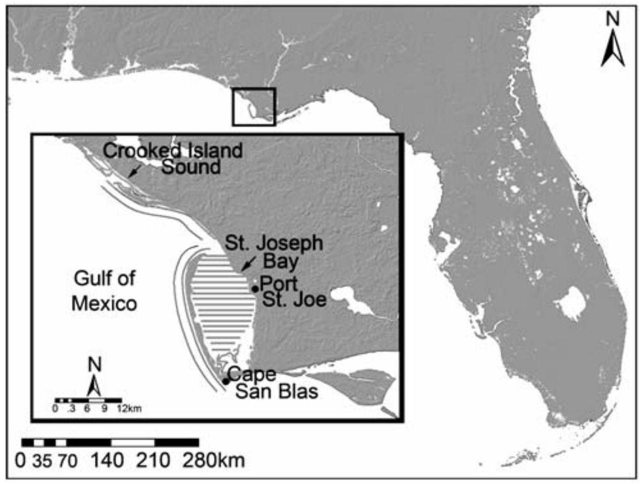

Fig. 1. St. Joseph Bay mark-recapture photo-ID survey region, including survey track lines.

Mark-recapture surveys were conducted across multiple seasons, including February/March, April, May and July 2005; February and September/October 2006 and June/July 2007. All transects were covered in a Beaufort Sea State of 3 or less for each survey, but the order of coverage was determined by random selection. All transects were also completed in as short a period of time as possible to meet the assumption of a closed population. Each mark-recapture survey was completed on average in 4.1 ±0.8 SD days, and the mark and recapture periods were separated by 1.2 ± 0.4 SD days on average.

A sighting was recorded when any dolphin was encountered. The total number of animals, numbers of calves including young-of-the-year and environmental data including salinity, water temperature, cloud cover, Beaufort Sea State, depth and geographic location were recorded for each sighting. Digital photographs were obtained of all individuals using a Nikon D-100 camera with 70-300m lens and downloaded onto a laptop computer in the lab. Dorsal fin images were cropped (*ACDSee* 7.0, ACD Systems, British Columbia, Canada) and graded on both distinctiveness of the dorsal fin and photographic quality, following the methods of Urian *et al.* (1999) and reviewed in Read *et al.* (2003) and Wilson *et al.* (1999). The distinctiveness rating (D1-D3) focused primarily on the notches along the trailing edge of the dorsal fin. Dolphins were given a D1 rating if their fin features were distinctive and most were still observable even in poor quality photos. A D2 rating was given to individuals with intermediate features (at least two distinguishing fin characteristics). D3 animals were those with few to no distinguishing characteristics. The photographic quality rating (Q1-Q3) focused on clarity, contrast, and angle of the fin to the photographer. A Q1 rating was given to a dorsal fin picture that was in perfect focus and that filled the entire field of the image. A Q2 rating was given when the image was still sharply focused but the fin occupied a smaller portion of the image. Q3 photos were those in which only a portion of a fin was included in the image or when the fin was not in sufficient focus. Two judges scored each image, one graded distinctiveness (BCB) and the other graded quality (SMN).

Using the quality and distinctive grades for images, a catalogue of fins was compiled (e.g. Urian *et al*., 1999). Q1-D1 and Q1-D2 photos were automatically added to the catalogue. Q2-D1 and Q2-D2 fins were not added until the fin was sighted twice, which ensured that lesser quality images were not added to the catalogue until they were proved matchable. Q3 images were not used for analysis. D3 images were used to help clarify the number of non-distinctive or clean individuals in a sighting.

In this study, a mark was considered a photograph of an individual dolphin's dorsal fin (Read *et al*., 2003; Urian *et al*., 1999; Wells *et al*., 1996; Williams *et al*., 1993; Wilson *et al*., 1999). A ratio of distinctive to non-distinctive ('clean') dolphins photographed in every sighting was calculated to estimate the proportion of marked versus unmarked animals during each survey season. This ratio is referred to as the distinctiveness rate.

Mark-recapture data analysis

When photographic mark-recapture methods are used to study bottlenose dolphin populations, the four assumptions of the closed, mark-recapture model (Seber, 1982) can be reasonably met if the sampling period is short, marks are not lost on recapture, and full survey coverage of the area allows for capture homogeneity (Read *et al*., 2003). The applicability of these assumptions was reviewed in Read *et al*. (2003) in their study of bottlenose dolphin abundance along North Carolina estuaries.

There are a number of closed and robust models that can be used to estimate population abundance (Thompson *et al*., 1998). The Chapman modification of the Lincoln-Petersen model, which assumptions require that of a closed population, was first applied to the data gathered during this study (Chapman, 1951). The data were then analysed using nine different closed and robust models that relaxed one or more of the closed population assumptions in the computer programs *MARK* and *CAPTURE* (Rexstad and Burnham, 1992; White *et al*., 1982). Model suitability was determined by having: (1) the lowest Akaike's Information Criterion (AIC) values (Burnham and Anderson, 1992); and (2) model parameters thought to be most representative of bottlenose dolphins along the northern Gulf coast of Florida (i.e. capture probabilities varying over time during and between survey periods, see results below). The two models that best fitted these requirements were the closed model (M_{th}) (Burnham and Overton, 1978; 1979; Darroch, 1958) and the robust 'Markovian Emigration' model (M_t) (Kendall *et al*., 1997).

The first model selected was the Chapman modification of the Lincoln-Petersen model (Chapman, 1951; Seber, 1982; Thompson *et al*., 1998). For each survey period, the sighting histories for all individuals were divided into two separate sampling occasions, the mark (n_1) and the recapture (n_2), where (n) equals the number of individuals identified during each sampling period. The total number of individuals seen during both mark and recapture equals (m_2). The abundance estimate (N_c), variance (var N_c), and standard error (SE) of the Chapman modification to the Lincoln-Petersen model were calculated as (Chapman, 1951):

$$N_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1 \quad (1)$$

$$\text{var}\, N_c = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \quad (2)$$

$$\text{SE} = \sqrt{\text{var}\, N_c} \quad (3)$$

The closed population model M_{th} was used because it allows animals to have different capture probabilities due to demographic variations, such as age or sex (model M_h) and it permits capture probabilities to vary by sample period (model M_t) (Burnham and Overton, 1978; 1979; Darroch, 1958; reviewed in Otis *et al*., 1978). This model is useful because it generates an abundance estimate while relaxing the assumption that all animals have equal capture probabilities. However, as the number of assumptions is reduced, variance in abundance estimates is increased (Thompson *et al*., 1998).

The robust design model (Pollock, 1982) uses characteristics of closed population abundance estimates and open population survival/emigration estimates (Kendall *et al*., 1997; reviewed in Pine *et al*., 2003; Pollock, 1982; Thompson *et al*., 1998). This approach permits abundance estimates to be determined during multiple, short term periods within a closed population model (M_t) and uses the Jolly-Seber open population model to estimate survivorship, emigration rates, and capture-recapture probabilities between the short term survey periods (reviewed in Pine *et al*., 2003; Pollock, 1982). The robust design model selected for this study was the 'Markovian Emigration' model, which permits unequal emigration and immigration rates across survey periods (Kendall *et al*., 1997). This model assumes that an animal 'remembers' that is has left the study area, and returns based on a time-dependent function (reviewed in Pine *et al*., 2003).

Abundance estimates from the closed (M_{th}) and robust 'Markovian Emigration' population models were based solely on the number of distinctive animals sighted during a survey period. The total population size (distinctive and non-distinctive individuals) was estimated as:

$$\tilde{N}_{\text{total}} = \tilde{N} / \Theta \quad (4)$$

where $\tilde{N}_{\text{total}}$=estimated total population size, $\tilde{N}$=mark-recapture estimate of distinctive individuals, and Θ=estimated proportion of distinctive individuals in each survey period (Read *et al*., 2003; Wilson *et al*., 1999).

Photo-identification site-fidelity indices

All photo-ID efforts within the survey region were used to calculate site-fidelity indices. These efforts began in April 2004, with a preliminary study to obtain genetic samples through biopsy darting. All photo-ID effort thus included the mark-recapture surveys, biopsy sampling, and radio tracking (see methods below). These efforts totalled 145 days over 15 months from April 2004 through July 2007.

To define a site-fidelity index for individual dolphins in the St. Joseph Bay region, the total number of sightings of each catalogued animal was determined. Then, for each mark-recapture photo-ID survey period, each observed individual was placed into one of five bins, based upon the total number of times it was sighted. The optimum bin size for each survey period was determined as:

$$BINSIZE = \frac{2*(IQR)}{\sqrt[3]{n}} \quad (5)$$

where IQR=the interquartile range of the number of sightings, and n=the total number of animals sighted. This estimator has been found to generate histograms that reliably represent the underlying density distribution of the data (Freedman and Diaconis, 1981). In this study, for each survey period, bin sizes were determined to be: (1) 1-8 sightings; (2) 9-17 sightings; (3) 18-26 sightings; (4) 27-35 sightings; and (5) 36 or greater sightings. These bins were used as the site fidelity index. A single factor analysis of variance (ANOVA) was used to test for differences in site-fidelity indices among seasons.

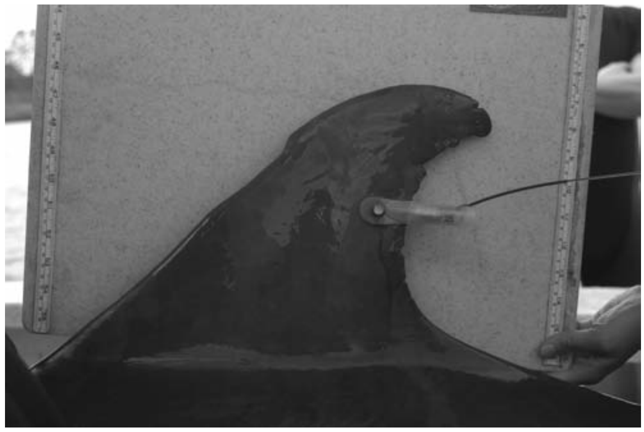

Fig. 2. Photograph of the dorsal fin of a temporarily captured and released bottlenose dolphin with radio transmitter mounted within bullet tag (Photo by S. Hofmann).

Distribution patterns of radio-tagged individuals

In April 2005 and July 2006, NOAA in collaboration with Chicago Zoological Society's Sarasota Dolphin Research Program and other partners, conducted bottlenose dolphin health assessment studies in the St. Joseph Bay region. The two goals of these studies were to: (1) carry out a detailed health examination of surviving bottlenose dolphins from the area impacted by the UMEs; and (2) deploy radio transmitters on bottlenose dolphins to obtain information on short-term movements. Only data from the second goal are presented here. Bottlenose dolphins in and around St. Joseph Bay, Florida were temporarily captured and restrained using practices similar to those implemented by the Sarasota Dolphin Research Program (Wells *et al*., 2004). Each individual was freeze-branded on the dorsal fin and/or body with a letter ('X') and two digit number ('01, 02, 03' etc.). Even numbers were given to males and odd numbers to females.

Twenty-three individuals across both health assessments were fitted with radio transmitters; one of these individuals was tagged in both years (April-July, n=9; July-October, n=15). The VHF radio transmitter (MM130, Backmount Transmitter, Advanced Telemetry Systems, Inc., Isanti, MN) was mounted in a modified plastic casing with a one-hole attachment, known as a bullet tag (Trac Pac, Ft. Walton Beach, FL). Prior to tag attachment, the dorsal fin was cleaned with ethanol and a chlorohexiderm scrub, and at the tag attachment point, a local anaesthetic (lidocaine 2% with epinephrine) was administered. The hole for tag attachment was made near the dorsal fin's trailing edge using a sterile 5mm biopsy punch. The tag was attached to the dorsal fin using a ¼" Delrin pin, threaded for ½" on each end, with non-stainless steel (corrodible) nuts on each side of the dorsal fin (Fig. 2). The VHF transmitters were tested prior to the health monitoring events and at sea level had a range of approximately 7-8km. The VHF transmitters were received over a 15km distance from an aircraft.

Radio-tracking was conducted using vessel, vehicle, and/or plane with the highest priority of visually locating each radio tagged dolphin daily (Fig. 3). Vessel tracking covered approximately 90km of coastline daily. When weather conditions were too poor to track by vessel (Beaufort Sea State >3), animal locations were triangulated from a land-based vehicle which covered approximately 150km of coastline per day. Since there were no prior data on dolphin movement patterns in this region, it was important to ascertain if individuals were leaving the areas covered by vessel or vehicle. Six aerial surveys covering over 270km per day were flown during the 2005 tracking period in a Cessna O-2A 'Skymaster'. To cover both estuarine and coastal waters, the aircraft stayed approximately 2km offshore of the coastline.

Radio-tracking of individuals ceased due to one of three conditions: the animal was sighted without its radio tag; the animal was sighted with its radio tag but the tag was not transmitting; or weather/logistical constraints did not permit continued tracking. During the 2005 tracking period, numerous hurricanes in the region prevented tracking after day 94. During the 2006 tracking period, only 2 tags remained functional after 75 days. The expense of remaining in the region to wait out the storm season outweighed the benefit of remaining to track the last two animals.

For each individual, the minimum number of tag transmission days was calculated. Ideally, this number was obtained by sighting an individual either without its radio tag attached, or with the radio tag still attached but non-functional, the day after a sighting of that animal with a functional tag. However, in most cases an individual was not observed the day after the last known transmission date. For these individuals an estimated final transmission date was calculated by counting the number of days between the last sighting with a functional tag and first sighting without a functional tag and dividing by two.

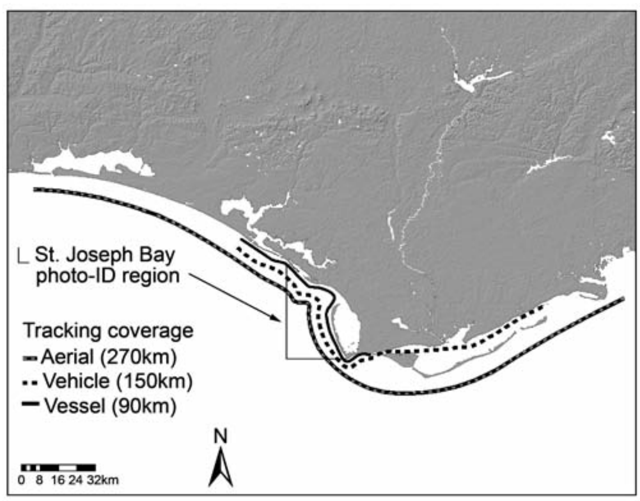

Fig. 3. Geographic ranges covered by vessel, vehicle, and plane during radio-tracking efforts. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region.

Locations for all radio-tagged individuals were determined by visual identification via vessel, triangulation from shore, or maximum signal strength via aerial tracking. All locations for each individual were plotted in *ArcMap* 9.2 (ESRI, Redlands, CA). The distribution pattern of a radio-tagged dolphin was defined as the maximum distance travelled along a shoreline between its farthest northwest and southeast tracking locations during each radio-tracking period. This linear method was selected over conventional home range analyses because it is a more conservative description of an individual's movement patterns and it better describes the study's temporal conditions and the nature of the animals' movements. The dolphins moved through a very narrow strip of coastline, such that measures of area are not as meaningful as linear measurements of range. In this study, the radio tracking was short-term (maximally 94 days; range 11-94 days) and although aerial and vehicle tracking extended the tracking coverage, complete distribution patterns may not have been obtained. Home range, the area that an individual conducts its normal activities such as resting, foraging, mating, and caring for young, is a term that has been applied to periods of time that encompass a greater percentage of an individual's life (Burt, 1943).

RESULTS

Mark-recapture abundance estimates

From April 2004 through July 2007, 313 individual bottlenose dolphins were identified in the St. Joseph Bay study region. The discovery curve of new individuals increased steeply until May 2005 and much more gradually thereafter (Fig. 4). The largest number of identifiable individuals was sighted in May 2005, including 129 previously identified and 73 newly identified individuals.

The number of identifiable dolphins directly counted during a photo-ID survey ranged from 45 to 202 (Table 1). The mean rate of distinctiveness across all seasons was 0.79±0.09 SD. The number of identifiable individuals was divided by the distinctiveness rate to estimate the total number of individuals (marked and unmarked) observed during each survey period (Table 1).

Closed population models (Lincoln-Petersen and M_{th}) were used to estimate dolphin abundance during each survey period (Fig. 5). Both models, respectively, estimated the highest abundances in May 2005 (313, 410) followed closely by April 2005 (240, 282) and September/October 2006 (237, 337). The lowest abundances occurred in June/July 2007 (84, 78), July 2005 (104, 105) and February 2006 (113, 105). The robust 'Markovian Emigration' model also estimated dolphin abundance to be highest in spring and autumn and lowest in summer and winter (Fig. 5). The lowest abundance estimates for the robust model were February 2006 (122) followed by July 2005 (131).

Photo-identification site-fidelity

For each survey period, each identified individual was placed into one of five sighting bins (i.e. site-fidelity indices) representing the total number of times that individual was sighted across all photo-ID efforts. To determine whether site-fidelity indices varied among seasons, histograms were plotted for each season using corresponding survey periods; spring (May 2005), summer (June/July 2007), autumn (September/October 2006) and winter (February 2006) (Figs 6a-6d). During May 2005 and September/October 2006, greater than 50% of the individuals were sighted only 1-8 times. In contrast, during June/July 2007 and February 2006, over 50% of the individuals were sighted 9-26 times. Site-fidelity indices differed significantly across seasons in the St. Joseph Bay region (*df*=3, *p*=1.62E-08, *F* =13.83).

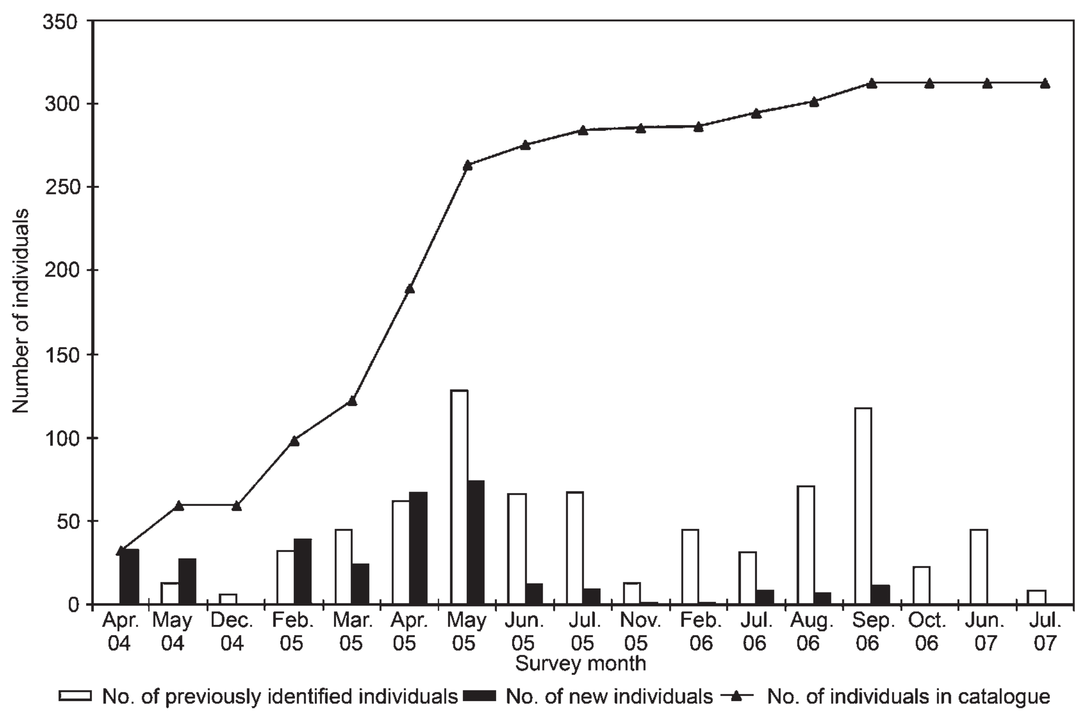

Fig. 4. Number of individuals sighted during all photo-ID efforts and discovery curve for bottlenose dolphins in the St. Joseph Bay region.

Table 1

Number of identified individuals sighted, distinctiveness rate, and estimate of total number of dolphins present during each mark-recapture survey season from photo-identification counts.

Field season	Feb./Mar 2005	Apr. 2005	May 2005	Jul. 2005	Feb. 2006	Sep./Oct. 2006	Jun./Jul. 2007
Number of identified (distinctively marked) dolphins sighted	122	144	202	83	47	176	45
Mark/distinctiveness rate	0.88	0.79	0.85	0.85	0.68	0.84	0.67
Estimate of total marked + unmarked dolphins	139	183	238	98	69	210	70

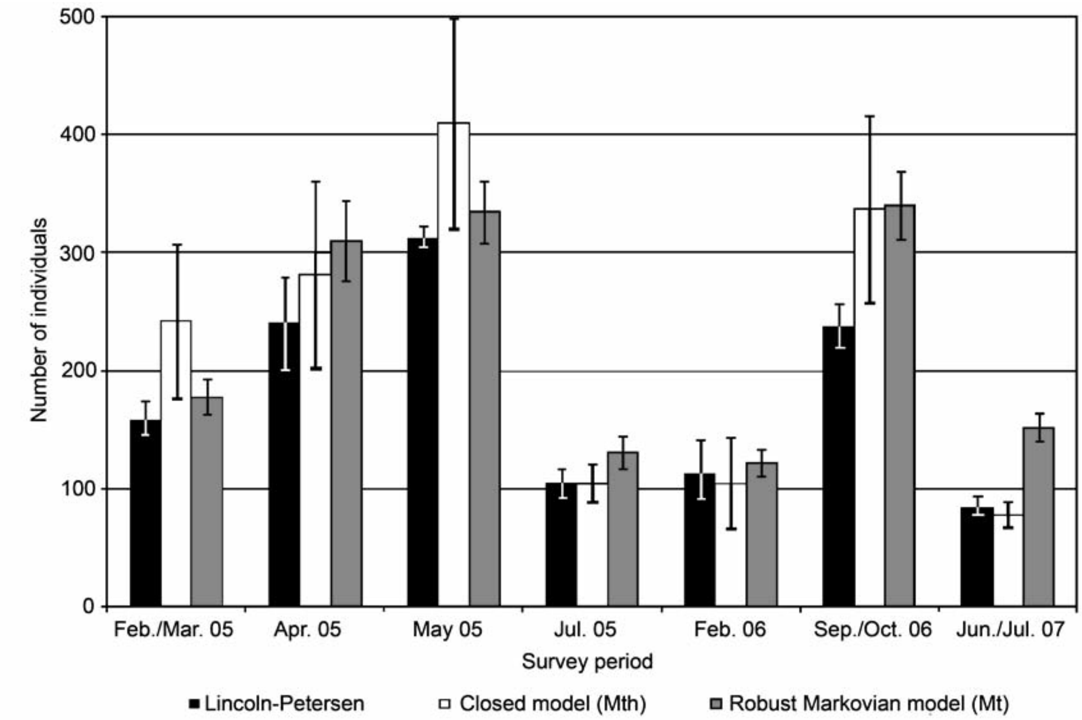

Fig. 5. Population size (± S.E.) estimated using closed (Lincoln-Petersen, M_{th}) and robust (Markovian Emigration) models for each survey period.

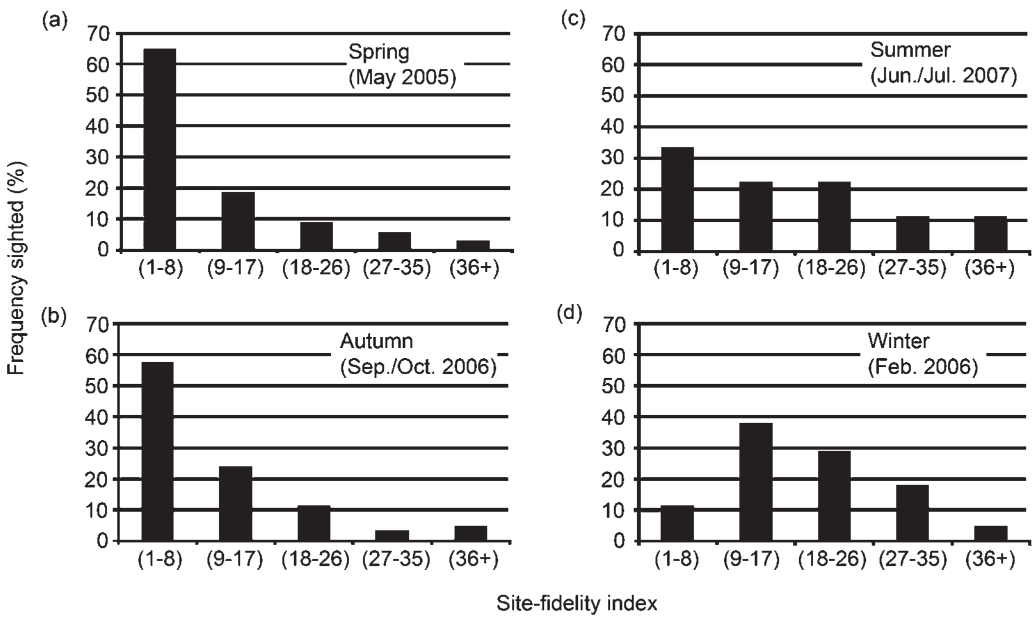

Fig. 6. Frequency of individuals sighted in each sighting bin (i.e. site fidelity index) during (a) May 2005, (b) June/July 2007, (c) September/October 2006 and (d) February 2006.

Distribution patterns

Twenty-three individual dolphins, eleven females (one female was tagged in both years) and twelve males, were radio-tagged during 2005 April 18-28 and 2006 July 17-28 (Table 2). In 2005, the average number of tag transmission days and number of fixed locations were higher than in 2006 (Table 2), but individuals with longer transmission periods and more fixed locations did not necessarily have larger distributional ranges.

In 2005, when tagging occurred in spring, two of the tagged dolphins (X09 and X13) travelled over 70km from their capture locations, and were infrequently seen within the survey region after their initial capture date (Fig. 7a). Two other individuals (X03and X08) had ranges that partially included the St. Joseph Bay photo-ID survey region (Fig. 7b). In contrast, dolphins X04 and X05 displayed relatively small maximal distances travelled and their ranges were completely within the St. Joseph Bay photo-ID survey region (Fig. 7c). In 2006, when tagging occurred in summer, only two dolphins (X23 and X29), ranged outside of the St. Joseph Bay photo-ID region but even these two were seen routinely within this area (Fig. 8a). The other eleven tagged dolphins were always located within the St. Joseph Bay survey region (Fig. 8b).

Five radio tagged individuals [X01, X02, and X11 (2005); X15 and X18 (2006)] were excluded from the radio tracking results described above. Dolphins X01 and X02 were exclusively observed begging for food from vessels in a small area just outside of the St. Joseph Bay region and all of their sightings during the radio-tracking period were restricted to this region. Because these individuals' distributions appeared to be strongly influenced by human activity, they were excluded from the analysis. Dolphin X11, an adult female, was radio tracked for 21 days before tag transmission ceased. During this period, her body condition deteriorated rapidly, she developed widespread skin lesions and her surfacings became progressively more lethargic. Because of this individual's decline in health, and eventual disappearance from the broader survey region, her tracking record was considered anomalous and was excluded. In 2006, dolphin X15 was resighted once post-capture, and dolphin X18 was monitored for only eight days post-capture, until tag transmissions ceased. For these reasons there were insufficient data to include dolphins X15 and X18 in the general analyses.

DISCUSSION

The goals of this study were to estimate bottlenose dolphin abundance, identify site-fidelity indices, and determine distribution patterns across seasons in a geographic region recently affected by several Unusual Mortality Events. Irrespective of how they were estimated, whether from direct counts of dolphins from photo-ID surveys, or from closed or robust population models, dolphin abundance varied across survey periods (Fig. 5). Abundance estimates increased between February/March 2005 and May 2005 survey periods. Between May and July 2005, abundance estimates decreased, and were low in February 2006 as well as June/July 2007. Abundance estimates were elevated again during September/October 2006. These data strongly suggest that in spring and autumn there is a movement of dolphins into the St. Joseph Bay region. These seasonally variable abundance estimates are similar to patterns seen for coastal bottlenose dolphins in other study sites within the western (Bräger, 1993; Fertl, 1994; Henningsen, 1991) and northern (Hubard *et al*., 2004) Gulf of Mexico.

Abundance estimates determined from the robust 'Markovian Emigration' model yielded seasonal patterns of abundance estimates similar to those of the closed population models (Fig. 5). Because this model allows for immigration and emigration rates to vary between survey periods, and for heterogeneity in capture probabilities within survey periods, the robust 'Markovian Emigration' model appears to best represent dolphin abundance in the St. Joseph Bay region. The radio-tracking results support this conclusion, because while some individuals (e.g. X05) were located consistently within the St. Joseph Bay region for the

Table 2

Tracking summaries for individual dolphins radio-tagged during 2005 and 2006. Linear distance of coastline represents maximum distance travelled along a shoreline between an individual's farthest northwest and southeast tracking locations.

Dolphin	Sex	Radio tagging date	Date of last radio signal	Min. no. days transmitting	No. of fixed locations	Linear distance of coastline (km)
2005						
X04	M	19 Apr.	08 Jul.	83	52	43
X03	F	20 Apr.	03 May	14	7	38
X05	F	20 Apr.	17 Jul.	91	44	42
X08	M	25 Apr.	25 Jul.	94	45	57
X09	F	25 Apr.	05 Jul.	74	23	105
X13	F	28 Apr.	05 Jul.	69	5	68
			Mean ± S.D.:	**71 ± 29**	**29 ± 21**	**59 ± 25**
2006						
X05	F	19 Jul.	17 Sep.	61	34	44
X10	M	19 Jul.	18 Aug.	30	26	44
X12	M	19 Jul.	02 Aug.	15	15	44
X06	M	20 Jul.	30 Jul.	11	11	44
X14	M	20 Jul.	10 Aug.	22	16	24
X16	M	20 Jul.	05 Aug.	17	14	12
X23	F	21 Jul.	01 Aug.	12	12	56
X25	F	25 Jul.	01 Oct.	75	37	50
X27	F	25 Jul.	01 Oct.	75	37	50
X20	M	27 Jul.	17 Sep.	61	23	53
X22	M	28 Jul.	01 Oct.	75	37	15
X24	M	28 Jul.	27 Aug.	29	10	43
X29	F	28 Jul.	26 Aug.	30	17	51
			Mean ± S.D.:	**35 ± 27**	**22 ± 11**	**40 ± 14**

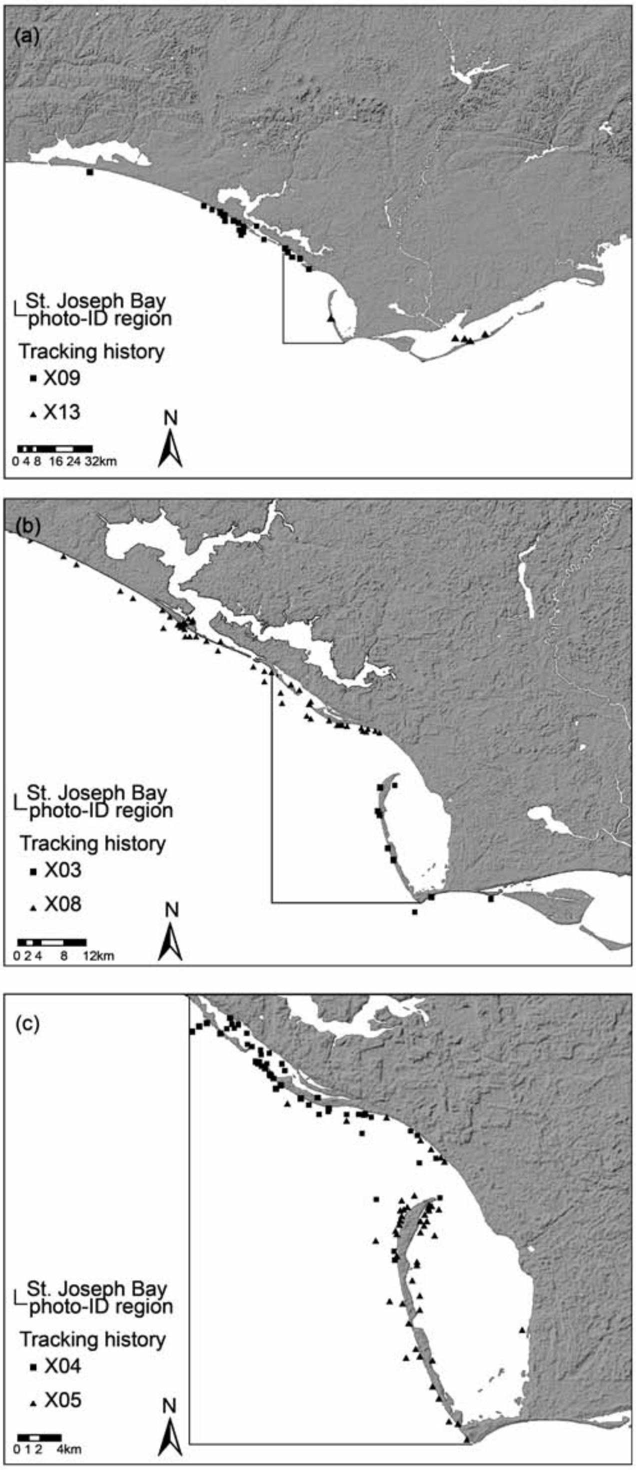

Fig. 7. Fixed locations of individually radio-tagged dolphins, during April-July 2005, whose distributions (a) extended outside, (b) partially overlapped, or (c) were completely within the St. Joseph Bay photo-ID region. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region.

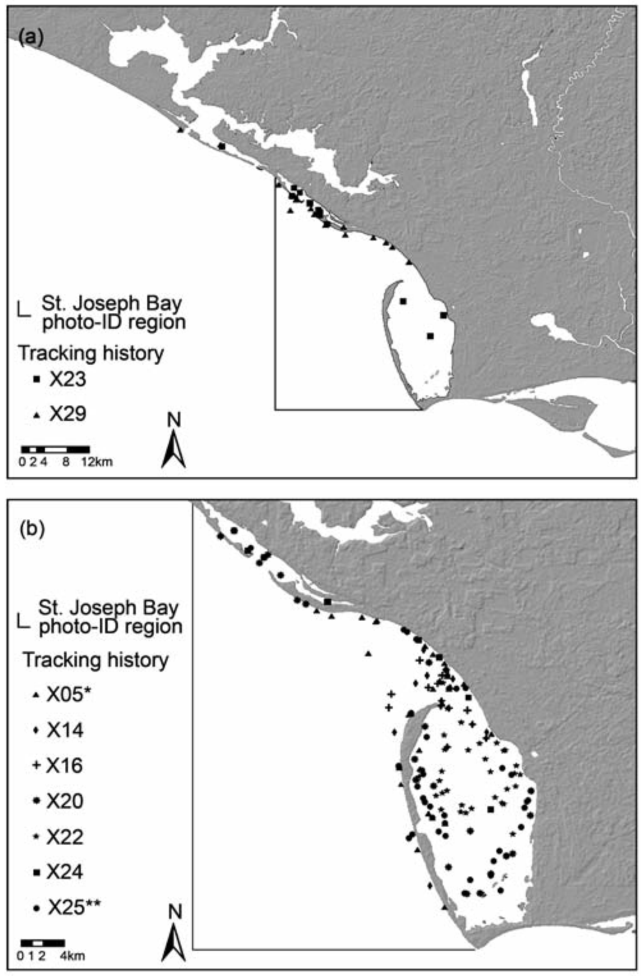

Fig. 8. Fixed locations of individually radio-tagged dolphins, during July-October 2006, whose distributions (a) partially overlapped, or (c) were completely within the St. Joseph Bay photo-ID region. The 'L' bracket displays the range of the St. Joseph Bay photo-ID region. *X05, X06, X10, and X12 had identical distribution patterns; **X25 and X27 had identical distribution patterns (X27 was a dependent calf of X25).

entirety of the study, other individuals (e.g. X09 and X13) clearly moved away from the region, and thus violated the assumptions of a closed population.

Individual sighting history data, which are temporally correlated with the abundance estimates, provide insight into site-fidelity patterns in the St. Joseph Bay region. In spring, when dolphin abundance estimates were highest, the percentage of individuals with the lowest site-fidelity index (1-8 sightings) was also highest (Fig. 6a). In contrast, in winter and summer, when abundance estimates were lowest, the majority of individuals sighted were those with moderate (9-17 sightings) to high (18-26 sightings) site-fidelity indices (Figs 6b and 6d). During autumn, the percentage of individuals with the lowest site-fidelity index (1-8 sightings) was again elevated as overall abundance within the survey region increased (Fig. 6c). These results suggest that during spring and autumn, when dolphin abundances are highest, the majority of dolphins sighted are visitors to the St. Joseph Bay region. In contrast, bottlenose dolphins seen in the winter and summer months are more likely to be sighted year-round.

These combined results would predict that at least some individuals radio-tagged in spring may have different movement patterns than those radio-tagged in summer, and this was indeed the case. Two individuals (X09 and X13) tagged in April 2005, ranged the farthest of all radio-tagged dolphins, with ranges extending largely outside of the St. Joseph Bay region. These results suggest that individuals sighted only in spring may have extended movement patterns both to the southeast and northwest of St. Joseph Bay. As would be predicted if there were year-round residents, though, some radio-tagged individuals displayed distributions that were completely within the St. Joseph Bay region (Fig. 7c). X05, a female captured and radio-tagged across seasons, for example, was located only within the focal, photo-ID study region.

In contrast, during July 2006, 11 of 13 radio-tagged individuals were sighted only within the St. Joseph Bay region. The two individuals who were sighted outside the focal study region still had the majority of their sightings (87-91%) within this region. These results suggest many individuals sighted in summer likely remain within the area for the entire season.

Estuarine bottlenose dolphin communities that have been studied in other regions tend to include between 60 and 150 individuals (Hubard *et al*., 2004; Wells, 1991; Williams *et al*., 1993; Wilson *et al*., 1999). The estimated size of the bottlenose dolphin community in Sarasota Bay, Florida, ranges between about 120 and 180 individuals (Wells, 2003, unpublished data). In the St. Joseph Bay region, during winter and summer, when the majority of dolphins display moderate to high site-fidelity indices, the robust 'Markovian' model estimates abundance at between 122 and 152 individuals. These results suggest that individuals sighted during winter and summer months may form a St. Joseph Bay estuarine dolphin community.

Coastal bottlenose dolphin stocks within other regions of the Gulf of Mexico have extended ranges (Beier, 2001; Lynn and Würsig, 2002) as well as geographic overlap with estuarine bottlenose dolphin communities (Fazioli *et al*., 2006). During spring and autumn, abundance estimates in the St. Joseph Bay region are two to three times higher than in summer and winter, and individuals sighted tend to have lower site-fidelity indices. Two individuals (X09, X13) radio-tagged in spring had distribution patterns extending over 70km from their capture locations. These two dolphins moved in opposite directions away from St. Joseph Bay after their initial capture, suggesting that there are likely multiple movement patterns that occur in spring and autumn. Whether this is a normal, long-term pattern for dolphins in this region, or if it is influenced by changes in dolphin abundance and density as a result of a series of UMEs is also unknown.

The data from this study are the first to describe seasonal abundance estimates, site-fidelity indices, and distribution patterns for bottlenose dolphins along Florida's northern Gulf of Mexico coast. The absence of such baseline data, prior to the UMEs, limits our understanding of the impacts of these events on bottlenose dolphins in the region at this time. However, several hypotheses can be generated about their potential impacts based upon the results of this study. The 2004 UME will be the focus of this discussion.

The 2004 UME may have had the greatest local impact on the St. Joseph Bay region, as 70% (75/107) of the mortalities occurred within or just outside St. Joseph Bay (NMFS, 2004). If this mortality event impacted only dolphins from the hypothesised St. Joseph Bay resident estuarine community, it would have reduced this group by at least 33-38%. Thus, in the years following this UME, we would hypothesise that higher birth rates and survivorship would be observed in the St. Joseph Bay dolphins, relative to other stable estuarine communities, as density-dependent responses to losses. In addition, there could be a potential increase in the number of visiting dolphins that are invading or staying within the St. Joseph Bay area. This could be tested through continuation of seasonal, mark-recapture, photo-ID surveys in the St. Joseph Bay region to determine if the changes in abundance, survivorship, and site-fidelity were indicative of a localized UME in the region.

An alternative hypothesis is that the 2004 UME, which occurred during March-April, a time of year when local abundance within the region is high, also affected seasonal visitors (Fig. 5). Thus, resident individuals of the St. Joseph Bay region, seasonal visitors, or both may have been impacted. If true, we would hypothesise a relatively reduced impact on the local St. Joseph Bay population and, perhaps, an elevated impact on the seasonal visitors travelling into the region. Continued short-term radio-tracking, targeting the St. Joseph Bay seasonal visitors, would provide insight into distribution patterns of these individuals. Extended mark-recapture, photo-ID surveys, targeting a broader geographic area along the northern Gulf coast of Florida could provide insights into changes in demographics and abundance of these seasonally transient bottlenose dolphins.

In summary, the results of this study demonstrate that the abundance of bottlenose dolphins in the St. Joseph Bay region varies seasonally. Dolphin abundance increases during the spring and autumn, and the majority of individuals sighted during these periods are those with low site-fidelity. In contrast, during the winter and summer, abundance estimates are lower and individuals demonstrate higher site-fidelity. These results suggest that the St. Joseph Bay region may have a resident community of dolphins (122-152 individuals) as well as seasonal visitors in spring and autumn, which may be part of the 'northern Gulf of Mexico' coastal stock.

NOAA Fisheries Service currently manages bottlenose dolphins along Gulf of Mexico estuaries as individual communities (Waring *et al*., 2007). Coastal bottlenose dolphins are managed as three separate stocks based on geographic location (Waring *et al*., 2007). This study supports the hypothesis of a resident, estuarine community in the St. Joseph Bay region that is seasonally visited by members of a potential coastal migratory stock. Future research is necessary to determine if these findings are consistent across other regions along the northern Gulf coast. It would be valuable, for example, to carry out systematic surveys, similar to the mark-recapture surveys conducted in this study, along other regions of the northern Gulf coast. Such efforts are currently underway in nearby Apalachicola Bay and St. Andrew's Bay (Tyson, 2008); T. Bouveroux, pers. comm. Ongoing analyses of genetic samples from biopsy darting of live individuals as well as samples from stranded animals will also provide additional insight into community/stock structure in the northern Gulf of Mexico, as they have elsewhere (Sellas *et al*., 2005; Torres *et al*., 2003). Continuation of mark-recapture photo-ID surveys in the St. Joseph Bay region is crucial to identify whether the seasonal fluctuations in abundance are an artifact of new animals filling in the gaps left by resident mortality, or a coastal migratory stock travelling through the region. Identifying the direct factors (foraging, reproductive, etc.) that cue seasonal abundance increases in the St. Joseph Bay region would also provide a better understanding of community structure of coastal bottlenose dolphins along the northern Gulf coast. All of these data are required to understand the impacts of future natural and/or anthropogenic catastrophic events on bottlenose dolphins in a region that seems unusually susceptible to such events.

ACKNOWLEDGEMENTS

This research was funded by NOAA Fisheries and the Disney Wildlife Conservation Fund and conducted under NMFS Scientific Research Permit Numbers 522-1569-01 and 522-1527-00 and UNCW IACUC permit number 2004-

012. We thank Marie Steele, Jean Huffman, Neil Jones and the rest of the staff at the St. Joseph Bay State Buffer Preserve for their generous hospitality, all the participants in the health assessments, Captain Dan Aspenleiter, Gerry Compeau, Jason Allen, Jennifer Yordy, Ron Hardy, Gene Stover and Eric Zolman for their logistic support; Aaron Barleycorn, Steve Roblee, Stephanie Schilling, Michelle Barbieri, Ross Kinard, Leigh Hardee, Leo Berninsone, Luciana Motta, and Reny Tyson for field work and data entry assistance; Bill Pine and Kim Bassos-Hull for assistance with the *MARK* and *CAPTURE* programs; Bob and Chung Murphy for aerial tracking survey support and Andrew Westgate for radio-tracking suggestions; the researchers of the FSU Oceanography Dolphin Research Program, the staff of the Sarasota Dolphin Research Program and the UNCW VAB Lab for continued support. The 'bullet' tag holder was designed and produced by Dr. Forrest Townsend and Frank Deckert, of Trac Pac, Inc. The manuscript benefited from useful comments by two anonymous reviewers.

REFERENCES

Barco, S.G., Swingle, W.M., McLellan, W.A., Harris, R.N. and Pabst, D.A. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Mar. Mammal Sci*. 15(2): 394-408.

Beier, A.G. 2001. Occurrence, distribution, and movements of outer coastline bottlenose dolphins off Galveston, Texas. MSc thesis. College Station, Texas A&M University. 97pp.

Bräger, S. 1993. Diurnal and seasonal behaviour patterns of bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci*. 9: 434-40.

Burnham, K.P. and Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to the modern data analysis. pp.16-30. *In*: McCullough, D.R. and Barret, R.H. (eds). *Wildlife 2001: Populations*. Elsevier Science Publishers, London.

Burnham, K.P. and Overton, W.S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65: 625-33.

Burnham, K.P. and Overton, W.S. 1979. Robust estimation of population when capture probabilities vary among animals. *Ecology* 60: 927-36.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal*. 30: 346-52.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *Univ. Calif. Publ. Statist*. 1: 131-60.

Darroch, J.N. 1958. The multiple-recapture census. I: Estimation of a closed population. *Biometrika* 45: 343-59.

Fazioli, K.L., Hofmann, S. and Wells, R.S. 2006. Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm*. 32: 212-22.

Fertl, D. 1994. Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texas J. Sci*. 46(4): 299-317.

Freedman, D. and Diaconis, P. 1981. On the histogram as a density estimator: L2 theory. *Probab. Theory Rel*. 57: 453-76.

Gruber, J.A. 1981. Ecology of the Atlantic bottlenose dolphin *Tursiops truncatus* in the Pass Cavalla area of Matagorda Bay. Master's thesis. Texas A&M University. 182pp.

Henningsen, T. 1991. Zur Verbreitung und Okologie des Grossen Tummlers (*Tursiops truncatus*) in Galveston, Texas. Diploma. Christian-Albrechts Universitat zu Kiel. 80pp.

Hubard, C.W., Maze-Foley, K., Mullin, K.D. and Schroeder, W.W. 2004. Seasonal abundance and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound. *Aquat. Mamm*. 30: 299-310.

Irvine, A.B., Scott, M.D., Wells, R.S. and Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish. Bull*. 79(4): 671-88.

Irwin, L.J. and Würsig, B. 2004. A small resident community of bottlenose dolphins, *Tursiops truncatus*, in Texas: monitoring recommendations. *Gulf of Mexico Science* 22: 13-21.

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

Lynn, S.K. and Würsig, B. 2002. Summer movement patterns of bottlenose dolphins in a Texas bay. *Gulf of Mexico Science* 20: 25-37.

Macdonald, D.W., Ball, F.G. and Hough, N.G. 1979. The evaluation of home range size and configuration using radio tracking data. pp.405-24. *In*: Amlaner, C.J. and Macdonald, D.W. (eds). *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, Oxford. 804pp.

Maze, K.S. and Würsig, B. 1999. Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site fidelity, and habitat use. *Aquat. Mamm*. 25(2): 91-103.

McLellan, W.A., Friedlander, A.S., Mead, J.G., Potter, C.W. and Pabst, D.A. 2002. Analysing 25 years of bottlenose dolphin (*Tursiops truncatus*) strandings along the Atlantic coast of the USA: do historic records support the coastal migratory stock hypothesis? *J. Cetacean Res. Manage*. 4(3): 297-304.

NMFS. 2004. Interim report on the bottlenose dolphin (*Tursiops truncatus*) unusual mortality even along the panhandle of Florida. 36pp. [Available from: NMFS, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149 and at *http://www.nmfs.noaa.gov/pr/health/mmume/event2004.htm*].

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr*. 62: 1-135.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J. and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* 28: 10-23.

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage*. 46: 757-60.

Read, A.J., Urian, K.W., Wilson, B. and Waples, D.M. 2003. Abundance of bottlenose dolphins in the bays, sounds and esturies of North Carolina. *Mar. Mammal Sci*. 19(1): 59-73.

Rexstad, E.A. and Burnham, K.P. 1992. *User's Guide for Interactive Program CAPTURE*. Colorado Coop. Fish and Wildl. Res. Unit, Colorado State University, Fort Collins. 29pp.

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd ed. Charles Griffin and Company Ltd., London. i-xvii+654pp.

Sellas, A.B., Wells, R.S. and Rosel, P.E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conserv. Genet*. 6: 715-28.

Shane, S. 1977. The population biology of the Atlantic bottlenose dolphin *Tursiops truncatus* in the Arkansas Pass area of Texas. MSc thesis. College Station,Texas A&M University. 238pp.

Shane, S.H. 1980. Occurrence, movements and distribution of bottlenose dolphins, *Tursiops truncatus*, in southern Texas. *Fish. Bull*. 78: 593-601.

Shane, S.H. 1990a. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. pp.245-66. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press Inc, San Diego. 653pp.

Shane, S.H. 1990b. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. pp.541-58. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, Inc, San Diego, CA.

Taylor, B.L. and Gerrodette, T. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conserv. Biol*. 7(3): 489-500.

Thompson, W.L., White, G.C. and Gowan, C. 1998. *Monitoring Vertebrate Populations*. Academic Press, San Diego. 365pp.

Torres, L.G., McLellan, W.A., Meagher, E. and Pabst, D.A. 2005. Seasonal distribution and relative abundance of bottlenose dolphins, *Tursiops truncatus*, along the US mid-Atlantic coast. *J. Cetacean Res. Manage*. 7(2): 153-62.

Torres, L.G., Rosel, P.E., D'Agrosa, C. and Read, A.J. 2003. Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Mar. Mammal Sci*. 19(3): 502-14.

Tyson, R. *Abundance of bottlenose dolphins (Tursiops truncatus) in the Big Bend of Florida, St. Vincent Sound to Alligator Harbor* 2008 [cited. MSc thesis. Florida State University, Tallahassee. xxpp.

Urian, K., Hohn, A.A. and Hansen, L.J. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic. Report of a workshop of catalog contributors. *NOAA Technical Memorandum NMFS-SEFSC* 425: 22pp. [Available from: *www.nmfs.gov*].

Waring, G.T., Josephson, E., Fairfield-Walsh, C.P. and Maze-Foley, K. 2007. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2007. *NOAA Tech. Mem*. NMFS-NE-194: 453pp. [Available at: *http://www.nefsc.noaa.gov/nefsc/publications/tm/tm194*].

Weller, D.W. 1998. Global and regional variation in the biology and behaviour of bottlenose dolphins. PhD thesis. Texas A&M University, College Station. 142pp.

Wells, R.S. 1986. Population structure of bottlenose dolphins: behavioural studies along the central west coast of Florida. NMFS Tech. Report 45-WCNF-5-00366 (unpublished). 70pp.

Wells, R.S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. pp.199-205. *In*: Pryor, K. and Norris, K.S. (eds). *Dolphin Societies, Discoveries and Puzzles*. University of California Press, Berkeley, California. 397pp.

Wells, R.S. 1994. Determination of bottlenose dolphin stock discreteness: application of a combined behavioural and genetic approach. pp.16-20. *In*: Wang, K.R., Payne, P.M. and Thayer, V.G. (eds). *Coastal stock(s) of Atlantic bottlenose dolphin: status review and management. Proceedings and recommendations from a workshop held in Beaufort, NC, 13-14 September 1993*. NOAA Technical Memorandum NMFS-OPR-4. 120pp.

Wells, R.S. 2003. Dolphin social complexity: lessons from long-term study and life history. pp.32-56. *In*: de Waal, F.B.M. and Tyack, P.L. (eds). *Animal Social Complexity: Intelligence, Culture, and Individualised Societies*. Harvard University Press, Cambridge, MA. 640pp.

Wells, R.S., Bassos, M.K., Urian, K.W., Shane, S.H., Owen, E.C.G., Weiss, C.F., Carr, W.J. and Scott, M.D. 1997. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Pine Island Sound, Florida: 1996. Final Contract Report to National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL. Contract No. 40-WCNF601958. 86pp. [Available from: *www.nmfs.gov*].

Wells, R.S., Rhinehart, H.L., Hansen, L.J., Sweeney, J.C., Townsend, F.I., Stone, R., Casper, D., Scott, M.D., Hohn, A.A., Rowles, T.K. and Howard, L. 2004. Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth* 1(3): 246-54.

Wells, R.S., Scott, M.D. and Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. pp.247-306. *In*: Genoways, H. (eds). *Current Mammalogy*. Plenum Press, New York. 519pp.

Wells, R.S., Urian, K.W., Read, A.J., Bassos, M.K., Carr, W.J. and Scott, M.D. 1996. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida: 1988-1993. *NOAA Tech. Mem*. NMFS-SEFSC-385: 25pp. [Available from: *www.nmfs.gov*].

Westgate, A.J. and Read, A.J. 1998. Applications of new technology to the conservation of small cetaceans. *Mar. Technol. Soc. J*. 32: 70-81.

White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.L. 1982. Capture-recapture and removal methods for sampling closed populations. *Biometrics* 39: 1122-23.

Williams, J.A., Dawson, S.M. and Slooten, E. 1993. Abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool*. 71: 2080-88.

Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl*. 9: 288-300.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198: 755-56.

Date received: September 2008
Date accepted: October 2008