Long-term site fidelity and seasonal abundance estimates of common bottlenose dolphins (*Tursiops truncatus*) along the southwest coast of Florida and responses to natural perturbations

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ABSTRACT

Information characterising site fidelity and abundance for common bottlenose dolphins (*Tursiops truncatus*) along the southwest coast of Florida is important for defining stock structure for management purposes. Long-term site fidelity and ranging patterns of bottlenose dolphins in Charlotte Harbor and Pine Island Sound, Florida were investigated using photo-ID data collected during 566 boat-based surveys from 1982 through 2007. Seasonal abundance estimates were generated from seven multi-week field seasons during 2001 through 2006, before and after a major hurricane and red tide event occurred in the area. In total, 1,154 distinctive dolphins were identified up to 34 times each with 84% of individuals resighted on more than one day. Multiple year residency rates were high with 81% of dolphins sighted in at least two years and 30% over ten or more years. Seventy-six percent of individuals with sightings on two or more days were observed in both summer and winter. Of 249 dolphins sighted on ten or more days in the study area, 83% were never observed outside the study area, indicating strong site-fidelity. Two years after a devastating Category 4 hurricane in 2004 and following two years of *Karenia brevis* harmful algal blooms, 94% of dolphins were observed in the same region within the study area and abundance estimates remained stable. Documenting range and site fidelity patterns of individuals over long periods of time is helpful for characterizing population structure and for examining changes attributable to environmental factors and perturbations such as hurricanes, harmful algal blooms and climate change.

KEYWORDS: COMMON BOTTLENOSE DOLPHIN; PHOTO-ID; SITE FIDELITY; ABUNDANCE ESTIMATE; MARK-RECAPTURE; CLIMATE CHANGE; NORTH AMERICA; NORTHERN HEMISPHERE

INTRODUCTION

Conservation strategies under the US Marine Mammal Protection Act (MMPA) aim to preserve marine mammal stock structure, specifying that '…population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part…' (US Marine Mammal Protection Act of 1972). Defining populations or stocks of marine mammals can be challenging due to the animals' often complex lives, large aquatic ranges and in some cases, continuous species distribution along coastlines. Stock identification can be derived from many types of information, including distribution and movements, population trends, morphological differences, genetic differences, contaminant and natural isotope loads, parasite differences and oceanographic habitat differences (Wade and Angliss, 1997).

Many marine mammals exhibit a distinct population structure, which may be most evident in their patterns of movement (Taylor, 2005). Stock boundaries for all US cetacean species have been designated by the National Marine Fisheries Service (NMFS) for stock assessment purposes, but in many cases there is uncertainty in the biological accuracy of these boundary decisions (Taylor, 2005). In the US Gulf of Mexico, 33 bay, sound and estuarine stocks were provisionally defined for common bottlenose dolphins (*Tursiops truncatus*), based primarily on geographical features rather than on documented movement patterns, genetics, or other kinds of biological data for the dolphins using the waters (e.g. Waring *et al.*, 2011). The focus stocks reported on in this paper, Lemon Bay (NFMS stock B21) and Gasparilla Sound, Charlotte Harbor, and Pine Island Sound (NMFS stocks B22–23) inhabit these estuaries and sounds in the southeastern portion of the Gulf. In addition to the bay, sound and estuarine stocks, NMFS has also defined three Northern Gulf of Mexico coastal bottlenose stocks (Western, Northern and Eastern) based on differences in climatic, coastal and oceanographic characteristics (Waring *et al.*, 2011).

Data for identifying bay, sound and estuarine bottlenose dolphin stocks and their interactions with Gulf coastal stocks are incomplete for much of the Gulf coast. However, information that is available indicates variability in stock structure across sites relative to residency to specific geographic regions. In order to optimise the utility of local residency as a guide for defining stocks relative to geographic features, several basic criteria should be met:

(1) residency should be pervasive throughout the study area;

(2) animals in the bay system should be resident to the area year-round, or they should be clearly identifiable as transients or seasonal residents, and therefore scored as members of different stocks;

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(3) residency should be long-term and stable through multiple generations; and

(4) provisional stock boundaries should contain most of the range of each of the putative residents.

With only a few exceptions, very few provisional stocks have been studied sufficiently to be able to examine them relative to all of these criteria.

The basic assumptions of stock identification based on residency in defined geographic regions have been examined in several areas of the Gulf through photographic identification (photo-ID) and tagging and tracking studies to document dolphin ranging patterns. Many of the findings to date support the concept of site fidelity for Gulf of Mexico dolphins in bays, sounds and estuaries, with year-round, multi-year residency exhibited by at least some individuals at nearly every site where photo-ID or tagging studies have been conducted (Texas: Bräger, 1993; Bräger *et al*., 1994; Fertl, 1994; Maze and Würsig, 1999; Shane, 1980; Würsig and Lynn, 1996. Florida: Balmer *et al*., 2008; Quintana-Rizzo and Wells, 2001; Wells, 1994). Typically, residents exhibit only limited movements through passes to the Gulf of Mexico, emphasising use of bay, sound or estuarine waters (Fazioli *et al.*, 2006; Irvine *et al.*, 1981; Maze and Würsig, 1999; Shane, 1980). This limited use of Gulf waters can be reflected in the ecology of the dolphins. For example, Barros and Wells (1998) noted that squid were not found in the diets of resident Sarasota Bay, Florida, dolphins, in contrast to the diets of non-resident dolphins stranded on nearby Gulf beaches. Stable isotope analyses further demonstrate dietary differences between dolphins using bays vs. Gulf of Mexico waters (Barros *et al.*, 2010). Residency patterns are somewhat more variable in certain regions of the Gulf such as northern Florida and the panhandle. In a more open estuarine system, the Cedar Keys, Florida region, Quintana-Rizzo and Wells (2001) identified a variety of residency patterns based on re-sighting rates ranging from 'frequent' to 'rare'. Balmer *et al.* (2008) identified year-round resident bottlenose dolphins in St. Joseph Bay, Florida, but also noted seasonal influxes of non-residents, including two radio tagged individuals that were tracked over 70km from their tagging location within the St. Joseph Bay region. These results suggested overlap between the St. Joseph Bay estuarine stock and the Northern Gulf of Mexico Northern stock. In northwestern Florida, NMFS has identified seven bay, sound and estuarine stocks adjacent to the Northern and Eastern Coastal stocks (Waring *et al.*, 2011) and several studies have suggested overlap between coastal and estuarine stocks, making stock delineations difficult.

In contrast to northwestern Florida, decades of research by the Sarasota Dolphin Research Program (SDRP), along the central west coast of Florida, involving photographic identification, tagging, tracking and genetic studies has led to documentation of strong site fidelity and long-term residency for many of the dolphins using these waters (Wells, 1994). In Sarasota Bay, research has been underway since 1970 to document population structure, ecology and demographics (Irvine *et al.*, 1981; Irvine and Wells, 1972; Scott *et al.*, 1990; Wells, 1991; 2003; 2009; Wells *et al.*, 1980). Over this period, on average, 89% of the sightings of resident dolphins occurred within Sarasota Bay (Wells, in review). Of those residents present in 2007 known to be at least 15 years old, 96% had been observed in the area over a span of at least 15 years, with some observed for as many as 37 years (Wells, In review).

Within Sarasota Bay, long-term (42 year) studies have monitored five concurrent generations of bottlenose dolphins totaling approximately 160 members (Wells, 2009). This long-term research has anchored our knowledge of bottlenose dolphin population ecology along the west coast of Florida and resulted in key behavioral observations and genetic findings that have led to the identification and description of biologically-based population units known as 'communities'. These communities are defined as regional societies of dolphins sharing ranges and social associates, but exhibiting genetic exchange with other social units (Wells *et al.*, 1999; Wells *et al.*, 1987). In some cases, communities can be considered to be essentially equivalent to stocks, with an explicit biological basis (Taylor, 2005). In addition to Sarasota Bay, dolphin communities have been identified just north in Tampa Bay, based on ranging and social association patterns and repeated identifications of some animals over several decades (Urian *et al.*, 2009; Wells *et al.*, 1996b). Bottlenose dolphin communities have also been identified for areas south of Sarasota Bay, including Lemon Bay, Gasparilla Sound, Charlotte Harbor and Pine Island Sound, suggesting the occurrence of long-term residency (Shane, 1990a; 2004; Wells *et al.*, 1996a; Wells *et al.*, 1997).

Building on data collected since 1982, recent research along the west coast of Florida has provided an opportunity to examine residency patterns relative to provisional stock boundaries and seasonal abundance trends. In 2001, intensive photo-ID surveys were initiated throughout Lemon Bay, Charlotte Harbor and Pine Island Sound (CHPIS) over multiple years and through multiple seasons to provide a basis for defining residency in this region and comparing population structure to provisional stock boundaries based largely on geography (Waring *et al.*, 2011). The more recent surveys have also provided unique opportunities for 'natural experiments' to test the strength of stability of residency patterns and trends in abundance in response to natural catastrophic events, including a devastating Category 4 hurricane and a series of severe *Karenia brevis* (red tide) harmful algal blooms, with resulting effects on water quality and dolphin prey species (Sallenger *et al.*, 2006; Stevens *et al.*, 2006; Tomasko *et al.*, 2006). The resulting data provide the first description of bottlenose dolphin population structure in CHPIS and allow for an evaluation of current stock designations.

METHODS

Study area

The Charlotte Harbor and Pine Island Sound study area (CHPIS) includes the enclosed bay waters eastward of the chain of barrier islands from the north end of Lemon Bay southward to San Carlos Bay as well as the shallow Gulf coastal waters around the passes between the barrier islands (Fig 1). The study area covers approximately 750 square kilometers and is composed of a variety of habitats, including highly productive seagrass meadows and mangrove shorelines, deep passes between barrier islands, dredged

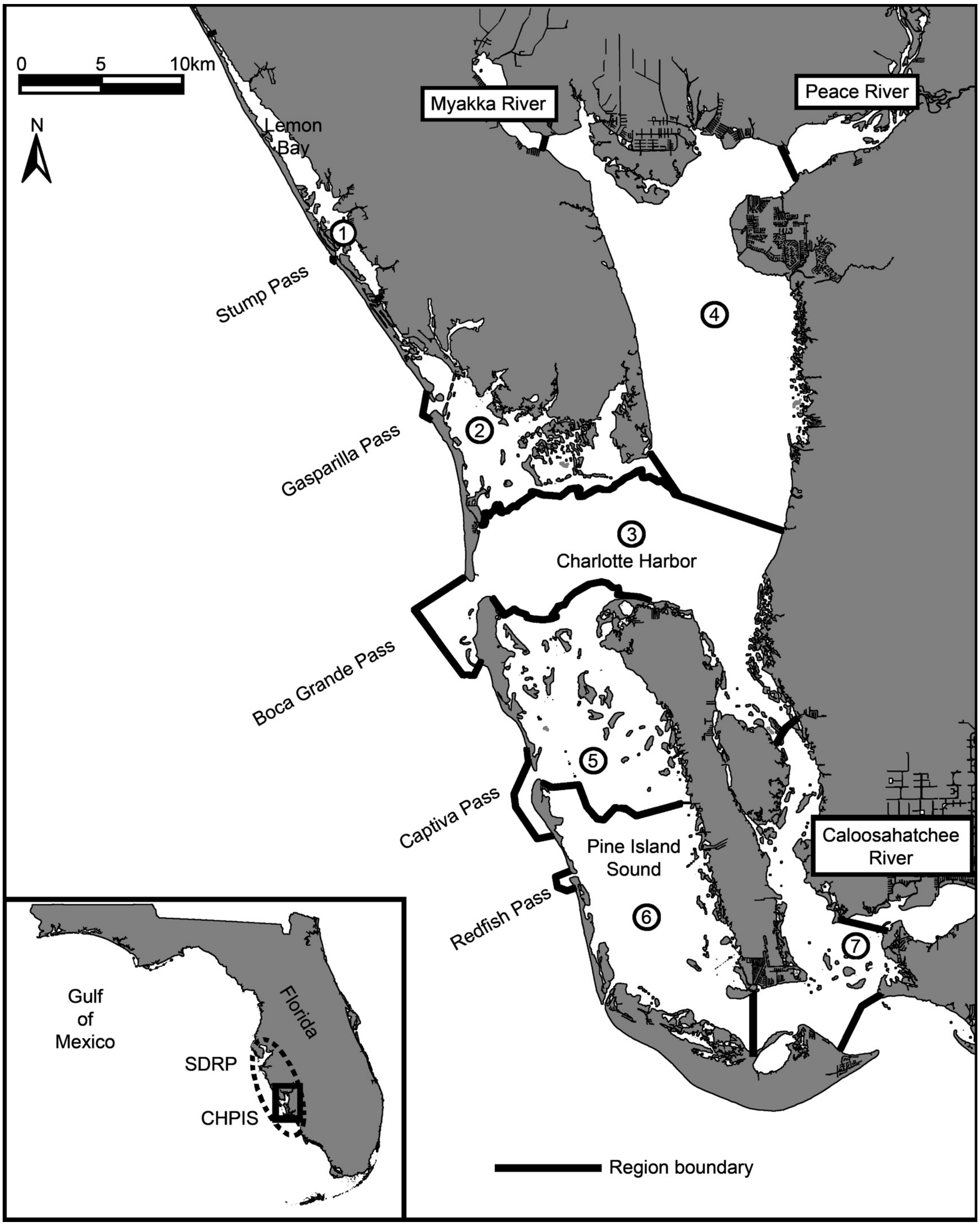

Fig. 1. Charlotte Harbor/Pine Island Sound (CHPIS) study area showing region boundaries, passes, barrier islands, rivers and bodies of water. On the inset map the larger Sarasota Dolphin Research Program (SDRP) study area is enclosed within a dashed line and smaller CHPIS study area is enclosed within a solid line.

channels, river mouths and open bays. The study area was divided into seven regions for assessment of survey effort, site fidelity and distribution following the segmentation scheme used in earlier Charlotte Harbor and Pine Island Sound surveys (Wells *et al.*, 1996a; Wells *et al.*, 1997) (Fig 1). Region 1, Lemon Bay, equates to NMFS stock designation B21, and Regions 2–7, including Gasparilla Sound, Charlotte Harbor, and Pine Island Sound are the same as NMFS stocks B22–23 (Waring *et al.*, 2011; Wells *et al.*, 1997).

Study background

Research on bottlenose dolphins in CHPIS has been conducted through both boat-based and aerial surveys since 1970. Tagging efforts occurred during 1970–71 (Irvine and Wells, 1972) and in 1984 (Wells, 1986). Aerial surveys designed to determine bottlenose dolphin abundance were conducted in CHPIS during 1975/76 (Odell and Reynolds, 1980) and by NMFS during 1980/81, 1983–86 and 1994 (Blaylock, 1995; Scott *et al.*, 1989; Thompson, 1981). A one-year study of the behavior and ecology of dolphins in southern Pine Island Sound and around Sanibel Island was initiated in 1985 (Shane, 1990a; 1990b) and opportunistic sighting data were collected through 1996 (Shane, 2004). Preliminary photo-ID began in 1982, but systematic surveys with the goal of determining trends in abundance were not conducted in the region until 1990 (Wells *et al.*, 1996a; Wells *et al.*, 1997). Surveys focused on the Charlotte Harbor region during 1990–94 (Wells *et al.*, 1996a) and on Pine Island Sound during 1996 (Wells *et al.*, 1997). The data reported here were collected during seasonal photo-ID surveys in Charlotte Harbor and Pine Island Sound conducted from 2001 through 2007 as well as long-term findings from combined datasets over all years.

Field effort and survey methodology

Building on the multi-week, multi-boat photo-ID surveys conducted during 1990–94 and 1996 (Wells *et al.*, 1996a; Wells *et al.*, 1997), as well as opportunistic surveys between major field sessions, seven seasonal multi-week surveys of CHPIS were conducted during September 2001–September 2006 using three vessels each day. The field sessions will be referred to as: September/October 2001 (summer 2001); January/February 2002 (winter 2002); September 2002 (summer 2002); February 2003 (winter 2003); September 2003 (summer 2003); February 2004 (winter 2004); and September 2006 (summer 2006). The survey design for these multi-week surveys used both line transects spaced 1km apart (followed with the aid of a GPS in open water areas) and contour transects (followed using a chart and depth contours in narrower areas). Both line transects and contour transects were randomly selected each day without replacement and conducted under Beaufort Sea State two or less when possible until the entire study area (all seven Regions) was completely surveyed (the Mark portion of the survey). The recapture portion of the survey was started 1.4 ± 0.5 SD days later on average. Both the Mark and Recapture survey segments took on average 8.0 ± 3.0 SD days each to complete. In addition, other opportunistic photo-ID survey and biopsy darting efforts were conducted between 2001 and 2007.

Surveys were conducted from 6–7m outboard-powered boats. Survey crews typically included a minimum of three people per boat and observer positions were rotated approximately every 60 minutes. While searching for dolphin groups, the boats operated at the slowest possible speed that would still allow the vessel to plane, typically 30–35km hr^{-1}, depending on the vessel. When groups were encountered, the boat slowed to match the speed of the dolphins and moved parallel to the group to obtain photographs.

Every dolphin group encountered along a survey route was approached for identification photographs (Scott *et al.*, 1990; Würsig and Jefferson, 1990). The research vessel remained with each dolphin group until the dorsal fin of each member of the group was photographed, or until conditions precluded complete coverage of the group. Prior to September 2003, primarily Nikon film camera systems with zoom-telephoto lenses (up to 300mm), motor drives, data backs and Kodachrome 64 color slide film were used. In February 2003, Nikon D100 digital camera systems with 80–300mm zoom-telephoto lenses were used complementary to the Nikon film camera systems on some surveys. Starting September 2003, only digital cameras were used.

A suite of data including date, time, location, activities, headings and environmental conditions were recorded for each sighting. In addition, minimum, maximum and best point estimates of numbers of total dolphins, calves (dolphins < about 80–85% adult size, typically swimming alongside an adult, a subset of the total number of dolphins) and young-of-the-year (as a subset of the number of calves) were also recorded.

Analysis of photographs

Each dorsal fin in a photograph was graded by two independent graders to characterise photographic quality and dorsal fin distinctiveness (Read *et al.*, 2003). Slides were examined using a high power (15x) loupe eyepiece. Digital photos were downloaded, labeled and cropped in *ACDSee* and/or *Adobe Photoshop*. Photograph quality rank was based on focus clarity, contrast, angle, portion of fin showing and percent of photograph frame filled (Q1 = excellent quality; Q2 = average quality; Q3 = poor quality). Dorsal fin distinctiveness was ranked on the strength of fin markings: D1 = dolphins with major fin markings, very distinctive fins with features evident in distant or poor quality photographs; D2 = dolphins with minor fin markings, fins with difficult to distinguish features in distant or poor photograph; D3 = dolphins with clean or non-distinctive fins. Dolphins with either a D1 or D2 fin were considered ‘marked’.

The best photograph of each individual with a D1 or D2 fin within each sighting was compared to our established SDRP Photo-Identification Catalog which includes individuals from Tampa Bay, Sarasota Bay, CHPIS and near-shore Gulf of Mexico coastal waters. When a match was made with a fin in the SDRP catalog, all photos were labeled with the dolphin’s unique code. The entire catalogue was searched by two staff members before a new animal was added to the catalog with a new code. As of August 2012, there were 3,425 marked individuals in the SDRP catalog, including the 276 dolphins identified by Shane (2004). Sexes of marked dolphins were determined through genetic analysis of skin samples obtained during biopsy darting efforts or visual examination during tagging efforts. In addition, marked dolphins were classified as female if they were sighted on three or more days with a calf surfacing alongside. All sighting and environmental data including identified individuals were entered into an Access database.

Sighting frequency and span of years seen

In order to examine sighting frequency and span of years seen, all photos (Q1, Q2, and Q3) of marked (D1 or D2) individuals sighted within the study area were used. The sighting frequency of all dolphins sighted since 1982 was limited to include only one sighting per individual per day within the study area. The span of years over which an individual was observed in the study area was calculated using only sightings by SDRP or Shane during 1982–2007 within the CHPIS study area.

Residency, site fidelity and ranging patterns

Residency patterns across years were determined by scoring the number of dolphins in the yearly catalogue during consecutive multi-week field season years (2001–04) that were identified in previous or subsequent years. Dolphins sighted in only a single survey year, and not in previous or subsequent years, were considered non-residents. Individuals were defined as year-round residents if they were sighted in at least one summer and one winter field season.

To quantify long-term site fidelity and ranging patterns in Charlotte Harbor and Pine Island Sound, individuals sighted on ten or more days within the study area were identified. The sighting locations of these individuals within the study area were examined to determine the prevalence of an individual's distribution pattern to a particular Region (1–7). In addition, the percentage of days sighted outside the study area was calculated.

Between the February 2004 and September 2006 surveys, several catastrophic events occurred in the CHPIS study area. These events provided opportunities to test the strength of site-fidelity and residency. On 13 August 2004, the eye wall of Category 4 Hurricane Charley passed through Regions 3, 4 and 5. These Regions, as well as the eastern half of Region 2, sustained devastating habitat damage (Stevens *et al.*, 2006). Beginning in February 2005, a severe *Karenia brevis* red tide harmful algal bloom impacted much of the west coast of Florida, including CHPIS, lasting for 11 months. Red tide impacted the CHPIS area again during September and October of 2006. This study examined how these combined events influenced site-fidelity by comparing sighting locations of dolphins observed at least ten days with at least one sighting before and after the hurricane and red tide events.

Abundance estimation

The number of dolphins inhabiting the study area was estimated for the seven primary field sessions conducted from September 2001 through September 2006. These data can be utilised to compare to other areas along Florida's west coast as well as establish baseline abundance estimates for the defined B22 and B23 Northern Gulf of Mexico bay, sound and estuarine stocks currently defined by NMFS (Waring *et al.*, 2011). The methods for estimating abundance in this study were based on similar studies performed on coastal and estuarine bottlenose dolphins (Balmer *et al.*, 2008; Chilvers and Corkeron, 2003; Read *et al.*, 2003; Speakman *et al.*, 2010; Williams *et al.*, 1993; Wilson *et al.*, 1999). The closed mark-recapture models (Seber, 1982) and robust design models (Pollock, 1982) used in this study follow the assumptions: (1) a demographically and geographically closed population (for abundance estimation), (2) homogeneity of capture probabilities; (3) marks are recognised on recapture; and (4) marks are not lost during the study period. These were reasonable assumptions for this study area as documented by previous mark-recapture studies conducted in this region (see Wells *et al.*, 1996a; Wells *et al.*, 1997). For all mark-recapture models only marked individuals with a D1 or D2 distinctiveness ranking and sightings with photo quality scores of Q1 or Q2 were utilised.

A Chapman modification of the Lincoln-Petersen model was used for the simplest mark-recapture abundance calculation (Chapman, 1951; Thompson *et al.*, 1998) where the mark period (n_1) was during the first set of completed transects and the recapture (n_2) was the second set of completed transects. Each (n) refers to the number of individuals photographically captured in each set and (m_2) refers to the number of individuals that were counted in both the mark and recapture period. The abundance estimate (N_c), variance (var N_c) and standard error (SE) were calculated as described in Chapman (1951):

$$N_c = ((n_1 + 1)(n_2 + 1)/(m_2 + 1)) - 1$$

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

$$SE = (\text{var } N_c)^{0.5}$$

A robust 'Markovian Emigration' population model to estimate abundance (see Balmer *et al.*, 2008 for a discussion of model suitability selection criteria and description for this type of application) was used because it permits abundance estimates to be determined during multiple, short-term survey periods within a closed population model (*Mt*) 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). Total abundance estimates of the entire CHPIS population (distinctive (D1 and D2) plus non-distinctive (D3)) were calculated using the Delta method (see Read *et al.*, 2003; Williams *et al.*, 1993; Wilson *et al.*, 1999).

RESULTS

Survey effort, group size and sighting frequency

Survey effort through the entire SDRP study area was essential for identifying northerly bounds for CHPIS residents. A total of 34,545 group sighting records were compiled during 1970 through 2007 with over 6,425 boat survey days within the entire SDRP programme study area of Tampa Bay, Sarasota Bay, CHPIS and the nearshore Gulf of Mexico coastal waters. As a subset of the above effort, 573 (9%) boat days occurred within the CHPIS study area, although the most intensive efforts in the region did not occur until 1990 (Fig. 2). Annual CHPIS survey effort relative to the rest of SDRP study area involved seven boat days (2%) in the 1970s, five (1%) in the 1980s, 223 (8%) in the 1990s and 338 (13%) in 2000–07.

Short-term site fidelity, at least, was suggested from early tagging studies. Few resightings during 1970/71 of tagged dolphins in CHPIS were documented because much of the field work was concentrated in Sarasota Bay and vicinity (Irvine and Wells, 1972). In addition, field efforts emphasised capture-release, allowing for only incidental resighting opportunities, and the durations of early tag attachments were limited, with a high rate of tag loss. The only documented re-identifications during this period involved two adult females tagged in northern Lemon Bay on 19 July 1971 and re-identified from fin scars two weeks later, within 1km of the original tagging site.

Most of the dolphins identified in CHPIS were observed on multiple occasions. Overall, 3,256 groups were approached ranging in size from one to 40 individuals (average group size = 5 ± 4.5 SD). Calves were present in 47% of dolphin groups (average group size with calves = 7 ± 5.2 SD; without calves = 3 ± 2.6 SD). In total, 1,154 different marked dolphins were identified within study area boundaries between 1982 through 2007. Of these, 139 (12%) were seen once, 766 (66%) were seen on two to nine days and 249 (22%) were seen on 10 or more days in the study area (Fig. 3).

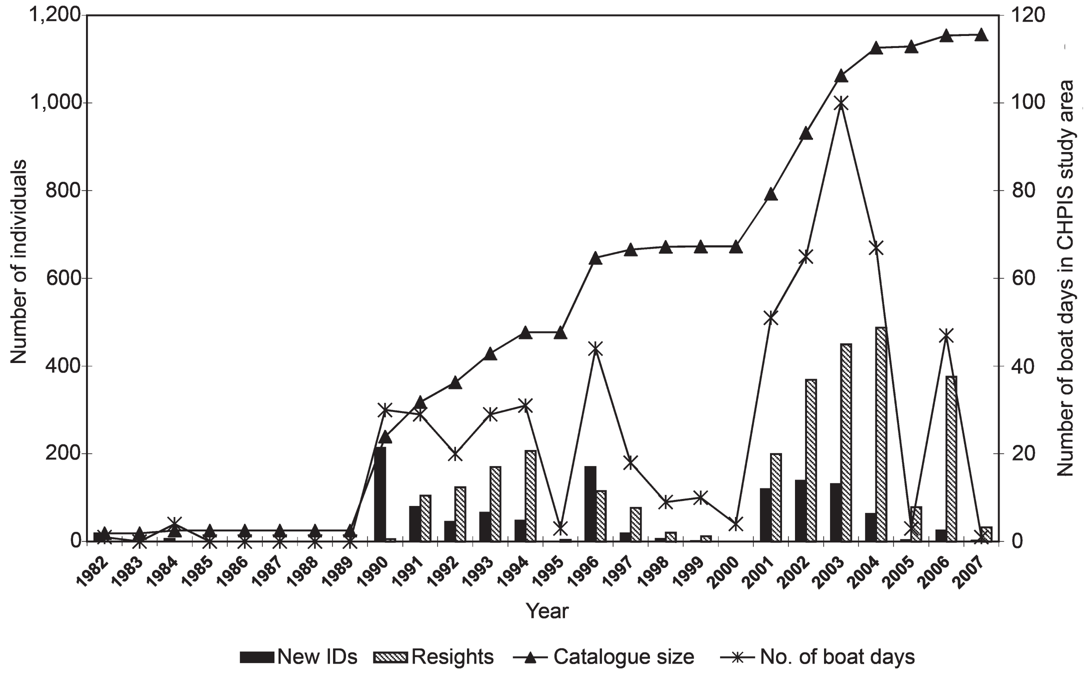

Fig. 2. Number of individuals (new and resights) sighted during all photo-identification efforts, discovery curve for dolphins in the study area and boat day effort.

Most of the dolphins in Charlotte Harbor and Pine Island Sound were identified by the end of the 2003 field seasons (Fig. 2). Understandably, the rate of discovery of new dolphins stabilised by the end of consecutive years with multi-week field seasons (1990–1994 and 2001–04, 2006) and increased when effort was expanded into new Regions (1996) or with the addition of winter field seasons (2002, 2003 and 2004).

Residency, site fidelity and ranging patterns

Overall, residency was defined on the basis of sightings in more than one year, and 937 individuals (81.2% of the total catalogue) met this criterion (Fig. 4). Of these, 332 individuals (28.8% of the total catalogue) were sighted over a span of two to four years and are considered short-term residents, 261 (22.6% of the total catalogue) were sighted during five to nine years and are considered moderate-term residents and 344 (29.8% of the total catalogue) were observed over ten or more years and are considered long-term residents. Two hundred and seventeen individuals (18.8%) were observed only within a single year (non-residents, or dolphins observed at the beginning or end of their residency). For dolphins that were sighted at least twice, most (76%) were year-round residents and were observed in at least one summer and one winter field season (Fig. 5).

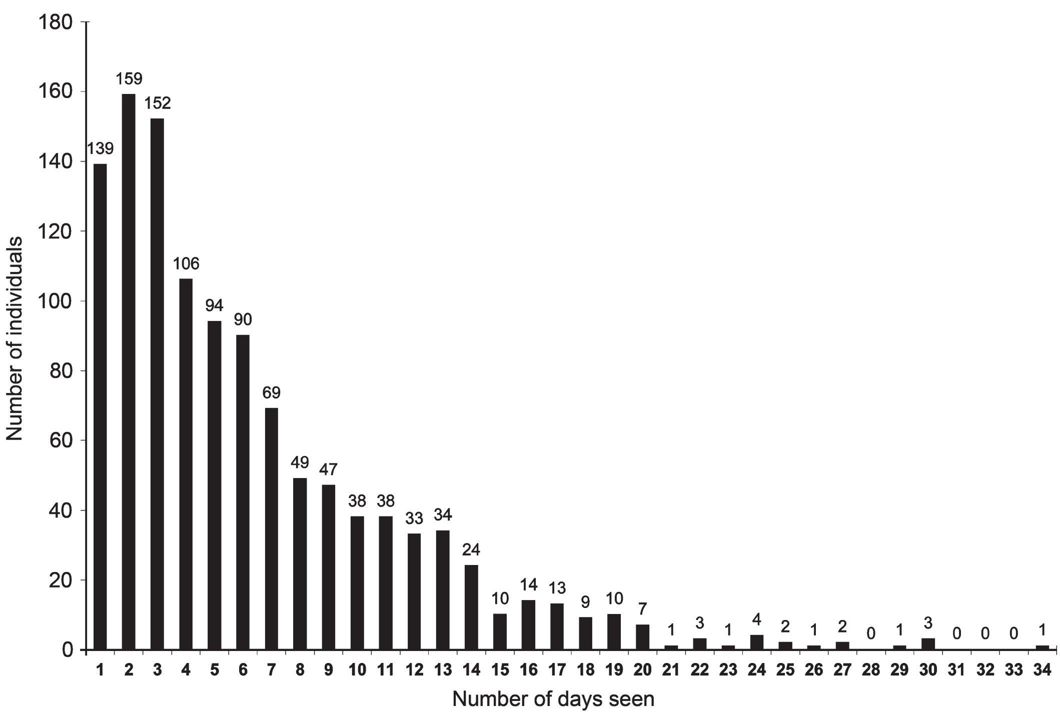

Fig. 3. Sighting frequency of individuals in the CHPIS study area 1982 to 2007

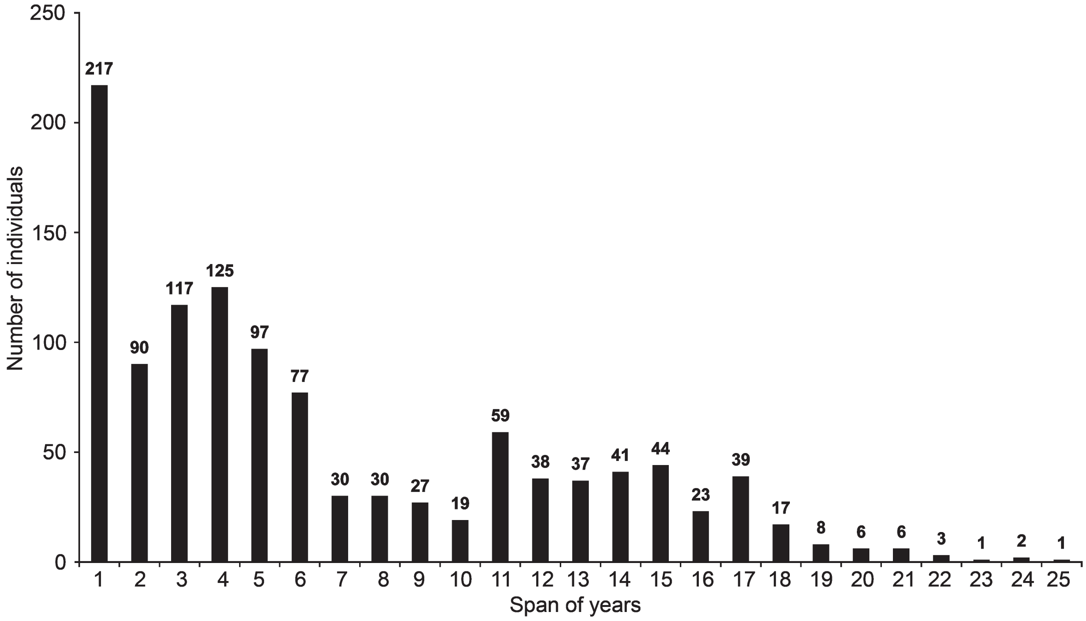

Fig. 4. Span of years seen within the CHPIS study area for 1,154 individuals.

In total, 249 dolphins were resighted on ten or more days in the study area and for further analyses are considered the '10+ sight' group, including 71 females, 30 males and 148 of unknown sex. Individuals from the 10+ sight group were resighted over a span of 3–24 years. Re-sighting patterns of these dolphins suggest strong site fidelity to CHPIS. Over 96% (240) had more than 80% of their sightings in the study area. More than 83% (207) were never observed outside of the ~750 km^2 CHPIS study area. Only nine individuals (3.6%) had at least 20% of their sightings outside of the study area.

Sighting distributions of all individuals in the SDRP catalogue sighted in the Gulf coastal waters adjacent to the CHPIS study area were compared to those of individuals sighted both in and out of the CHPIS study area to assess the frequency of occurrence of Gulf dolphins inside the study area. In total, 287 individuals were sighted at least once in adjacent Gulf coastal waters but were never observed within the study area, and 180 individuals were sighted both in and out of the study area, with 66 of these observed on ten or more days. Of these 66 dolphins, 22 had more than 50% of their sightings outside the study area. These 22 dolphins were observed to the north of the study area in either Sarasota Bay (an area with intensive monthly survey effort) or Tampa Bay.

On a smaller scale, dolphins from the 10+ sight group demonstrated varying degrees of site-fidelity to particular Regions within the CHPIS study area. More than half (57%) were sighted in just one or two Regions in the study area. Only 2.4% were observed in five or more Regions. Table 1 shows the distribution of sightings of these dolphins across the Regions. From the 10+ sight group, four dolphins were seen exclusively in Region 1 (Lemon Bay, NMFS stock B21), while the remaining 245 were seen in Regions 2–7 (Gasparilla Sound, Charlotte Harbor, Pine Island Sound, San Carlos Pass, NMFS stock B22–23). Not surprisingly, dolphins were typically observed most frequently in adjacent regions.

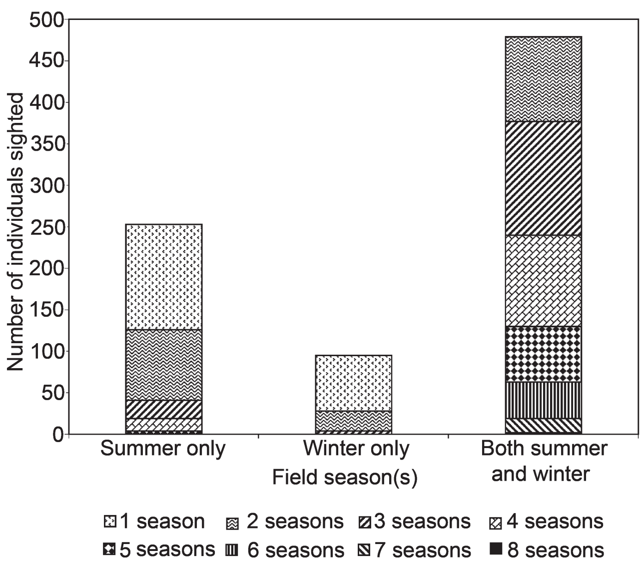

Fig. 5. Number of individuals seen in summer only, winter only, or both summer and winter field seasons within the CHPIS study area.

Hurricane Charley in 2004 and subsequent red tides in 2005/06 did not appear to have long-term impacts on individual site fidelity within the study area. Of the 192 dolphins seen on at least ten days and with sightings both before and after Hurricane Charley, 94.3% (181) were resighted within the same Region. Examples of this Regional and long-term site fidelity for four of these individuals are illustrated in Figure 6 and they are representative of the site fidelity patterns of the other 177 dolphins.

Dolphins using the CHPIS region are typically seen in multiple consecutive years and only a small percentage (<10%) of those observed are not sighted in multiple years. Years 2002 and 2003 were used to calculate residency on a percentage basis (since those years included multi-week surveys with previous and subsequent multi-week survey years including the entire CHPIS study area). For the 508 dolphins identified in 2002, 252 (49.6%) were observed in 2001 and 371 (73.0%) in 2003. For the 581 dolphins

Table 1

Number of dolphins from the 10+ sight group that were observed in each Region. The bold values in the matrix represent the number of individuals seen exclusively in that Region. The other values represent the number of individuals that share sightings amongst the Regions.

	# IDS	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	Region 7
Region 1	**39**	**4 (10%)**	29 (74%)	18 (46%)	3 (8%)	7 (18%)	1 (3%)	1 (3%)
Region 2	**79**	29 (37%)	**2 (3%)**	64 (81%)	30 (38%)	30 (38%)	8 (10%)	3 (4%)
Region 3	**145**	18 (12%)	64 (44%)	**0 (0%)**	58 (40%)	86 (59%)	40 (28%)	14 (10%)
Region 4	**65**	3 (5%)	30 (46%)	58 (89%)	**6 (9%)**	21 (32%)	7 (11%)	6 (9%)
Region 5	**147**	7 (5%)	30 (20%)	86 (59%)	21 (14%)	**1 (1%)**	92 (63%)	17 12%)
Region 6	**112**	1 (1%)	8 (7%)	40 (36%)	7 (6%)	92 (82%)	**6 (5%)**	26 (23%)
Region 7	**30**	1 (3%)	1 (10%)	14 (47%)	6 (20%)	17 (57%)	26 (87%)	**0 (0%)**

identified in 2003, 371 (64.0%) were observed in 2002 and 406 (70.0%) in 2004. Thirty nine dolphins (7.7%) were only seen in 2002 and 58 (10.0%) were only seen in 2003.

Abundance estimates

The number of marked dolphins directly counted during each of the seven primary field seasons ranged from a low of 223 in winter 2002 to a high of 345 in winter 2004 (Table 2). The calculated distinctiveness (or marked proportion) rate ranged from 62% in winter 2002 to 78% in winter 2004 (Table 2). Seasonal abundance estimates derived from both the Lincoln-Petersen and robust design models (Markovian) and adjusted by the Delta method ranged from the lowest estimate, in summer 2001 (N = 636, 95% CI = 532–793) to the highest in summer 2002 (N = 848, 95% CI = 706–1,036) (Fig. 7). During summer 2006, two years after Hurricane Charley, the estimate was 826 (95% CI = 710–989) (Fig. 7).

DISCUSSION

From a conservation and management perspective, quantitative information about the site fidelity, residency, ranging patterns and abundance trends of dolphins using a particular geographic area is helpful for defining management approaches. Our findings indicate that a large majority of the dolphins that use Charlotte Harbor and Pine Island Sound appear to be both long-term and year-round residents with strong regional site fidelity. This supports the NMFS designation of this area as a geographic management unit. Most of the resident CHPIS dolphins have never been observed outside study area boundaries to the west and north despite intensive SDRP survey effort in these regions. The Gulf and bay waters to the south of CHPIS have not been extensively surveyed for bottlenose dolphins and should be an area considered for future studies. Our residency findings from 2001–07 are consistent with, and expand upon, earlier findings from the CHPIS area (Wells *et al.*, 1996a; Wells *et al.*, 1997) as well as other nearby west coast Florida estuaries such as Tampa Bay (Urian *et al.*, 2009; Wells *et al.*, 1996b) and Sarasota Bay (Wells, 1986; Wells, 1994; Wells, 2009). Findings from multiple complementary studies have supported this differentiation through genetic analyses (Duffield and Wells, 2002; Duffield and Wells, 1991; Sellas *et al.*, 2005; Wells, 1986) and stable isotopes (Barros *et al.*, 2010). The similarity of site fidelity and residency patterns of bottlenose dolphins in west Florida estuaries, as well as the overall low level of movement of individuals between these bordering estuaries, is remarkable. These findings extend the mosaic of long-term resident bottlenose dolphin communities along the west coast of Florida from at least Old Tampa Bay, through Pine Island Sound, a distance of nearly 200 km of contiguous inshore waters.

The observed level of site fidelity in CHPIS supports the general approach of the National Marine Fisheries Service to identify bay, sound and estuarine stocks at least in part on the basis of ranging patterns relative to geographic features. However, our findings suggest that current management unit boundaries may not be entirely appropriate. In particular, there was a lack of evidence to support the current identification of the NMFS management unit B21 (Lemon Bay) as being discrete from B22–23 (Gasparilla Sound, Charlotte Harbor, and Pine Island Sound). The data indicate that most dolphins using Lemon Bay range between the two management units. Of the 249 dolphins sighted 10 or more times within CHPIS, 39 of these individuals were seen in Lemon Bay but only four of these dolphins were seen in Lemon Bay exclusively. The remaining 35 individuals ranged through both B21 and B22–23. Therefore, combining B21 with B22–23 is recommended, until such time as more detailed analyses may yield further information on fine scale stock structure, as has been done recently for a comparable 852 km^2 estuarine system to the north, Tampa Bay (Urian *et al.*, 2009). Similar to Tampa Bay dolphins, CHPIS dolphins typically range into adjacent Regions within the larger CHPIS ~750km^2 study area complex but not throughout the entire area (87.9% in three or fewer Regions).

Based on the above findings, dolphins in the CHPIS study area meet the assumptions needed to estimate abundance using closed population models. By using a dorsal fin grading system to characterise photographic quality and dorsal fin distinctiveness (i.e Read *et al.*, 2003) and a rigorous two person photo-ID cross-checking system, we have minimized the possibility of marks not being detected for recapture and increased the chances of changed fins being detected. Individuals with more subtle D2 fin markings were seen over the same span of time and with similar numbers of sightings as D1 individuals with more extensive fin markings, meeting the assumption of homogeneity of recapture.

Our most recent (2006) best estimate of abundance for the combined B21–22–23 management unit is 826 dolphins (95% CI = 710–989). Abundance of dolphins in CHPIS remained relatively stable across years and seasons during 2001 through 2006. The 2001–06 abundance estimates are much greater than that reported for 1994 in NMFS Stock Assessment Reports for the CHPIS study area. The best estimates of dolphin abundance from NMFS aerial surveys

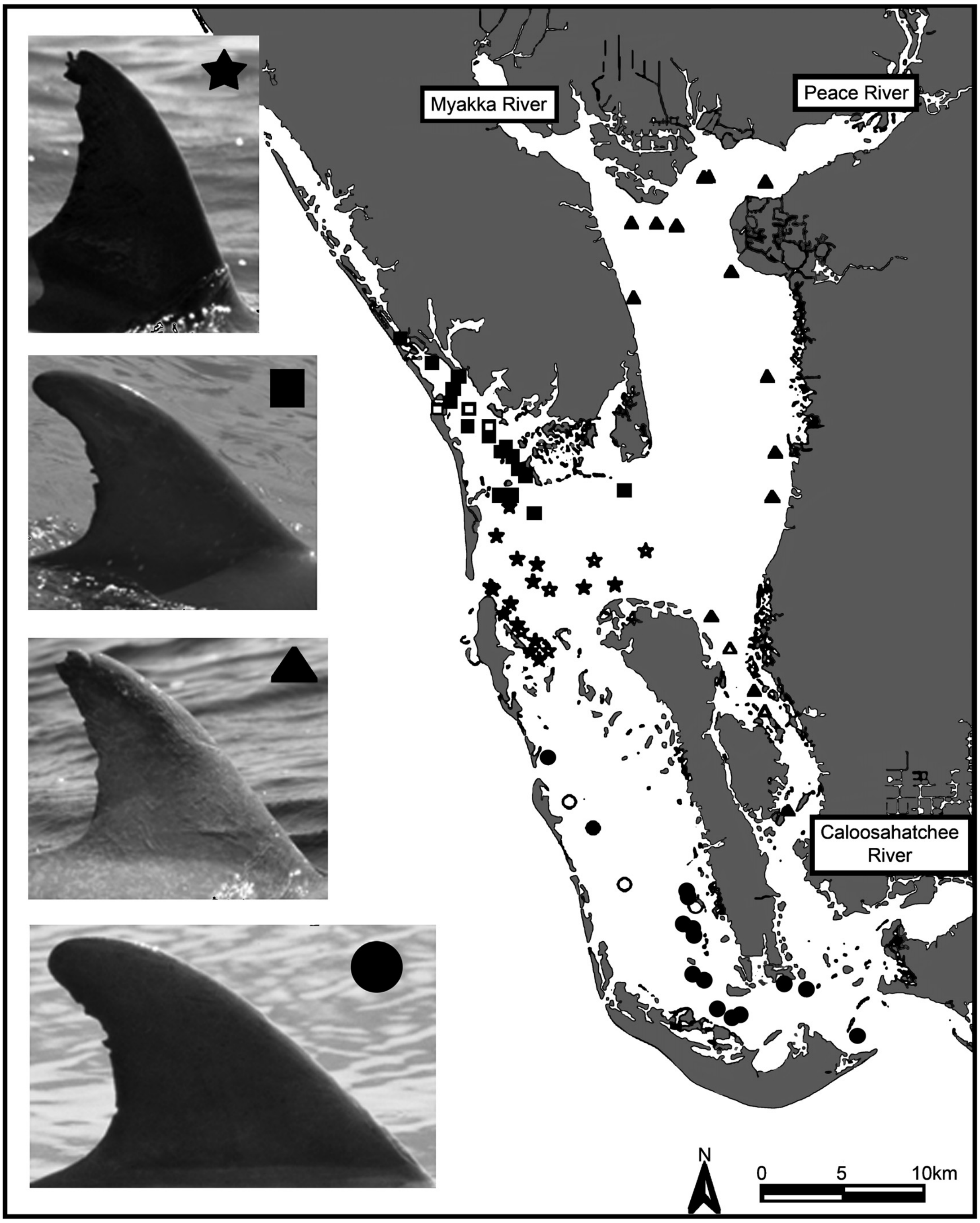

Fig. 6. Sighting distributions of four individuals, RHNO (star), SMRF (square), SNST (triangle) and WVPN (circle) both before and after Hurricane Charley (13 August 2004). Closed symbols represent sightings prior to Hurricane Charley and open symbols represent sightings after Hurricane Charley.

Table 2

Number of marked (D1 or D2 grade) individuals sighted, distinctiveness rate, and estimate of total number of dolphins in CHPIS study area during each field season.

Field season	Summer 2001	Winter 2002	Summer 2002	Winter 2003	Summer 2003	Winter 2004	Summer 2006
Number of marked dolphins identified	247	223	322	283	328	345	330
Distinctiveness rate	0.69	0.62	0.65	0.71	0.75	0.78	0.70
Mark-proportion estimate of marked + unmarked dolphins	358	360	495	399	437	442	471
Total abundance estimate (Robust Markovian) of marked + unmarked dolphins	636	848	892	777	757	868	826
Standard deviation	65.3	83.7	82.8	82.5	62.6	72.6	70.3
Coefficient of variation	0.10	0.10	0.09	0.11	0.08	0.08	0.09
Upper 95% confidence limit	793	1,036	1,086	974	903	1,034	989
Lower 95% confidence limit	532	706	757	645	654	746	710

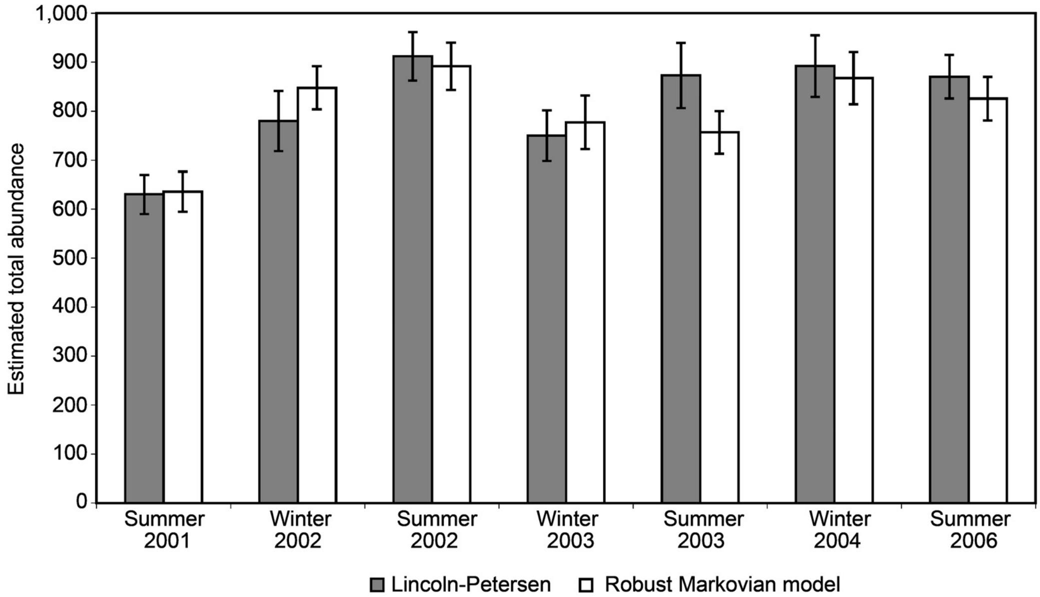

Fig. 7. Population size (±SE) estimated using closed (Lincoln-Petersen) and robust (Markovian Emigration) models for each survey season.

as of 1994 was 0 for Lemon Bay (B-21), and 209 for Charlotte Harbor, Pine Island Sound and Gasparilla Sound (B22–23) (Waring *et al.*, 2011). During SDRP's previous boat-based photo-ID efforts, abundance estimates in Charlotte Harbor (Regions 1–5) were relatively stable between 1990–94, with a minimum estimate of 238 (95% CI = 198–278) in 1992 and a maximum estimate of 385 (95% CI = 341–429) in 1994 (Wells *et al.*, 1996a). The abundance estimate for Pine Island Sound (Regions 6 and 7) in 1996 was 247 (95% CI = 228–266) (Wells *et al.*, 1997). Abundance estimates from the current study exceed those from previous aerial and vessel surveys in the region, but it is unclear whether this represents a true increase or if it is an artifact of field and analytical methodological differences across the decades.

The dolphins in CHPIS showed no evidence of long-term impacts from large-scale environmental perturbations. In 2004, Hurricane Charley devastated the shoreline, terrestrial flora and man-made structures along its path, changed the physiography of the estuary, and washed tremendous quantities of biological and chemical pollution into CHPIS. Major red tide events impacted the region in 2005 and 2006, killing massive quantities of fish. In spite of these perturbations, dolphin abundance in 2006 was within, or slightly greater than the 2001–04 abundance estimates, and 94% of dolphins were re-sighted within their previous ranges. Sharks and other fish in the CHPIS system and nearby estuaries were also found to resume normal patterns following hurricanes (Heupel *et al.*, 2003; Locascio and Mann, 2005; Ubeda *et al.*, 2009).

The apparent resilience and stability of the dolphins of CHPIS to multiple potentially catastrophic natural perturbations is noteworthy in light of reported responses elsewhere. Miller *et al.* (2010) suggested that Mississippi Sound experienced an increase in bottlenose dolphin reproduction in the two years following Hurricane Katrina, but the time series used by Miller and colleagues is too brief to confirm changes beyond the normal multi-year cycle of interannual reproductive variability. For comparison, annual bottlenose dolphin fecundity in Sarasota Bay, Florida, can vary by nearly an order of magnitude from one year to another (Wells and Scott, 1990), a range of variability greater than the changes in calf encounters reported by Miller *et al.* (2010). Elliser and Herzing (2011) reported dramatic changes to the social structure of bottlenose dolphins over the Little Bahama Banks in response to passage of two major hurricanes over a three week period in 2004. The long-term resident community experienced the disappearance of 30% of its members with the storms. Subsequently, approximately the same number of individuals immigrated into the population, and a new social structure was established.

Bottlenose dolphin responses to *K. brevis* blooms vary depending on the strength, duration and spatial coverage of the bloom, among other factors. In the northern Gulf of Mexico, several recent federally declared Unusual Mortality Events involving the deaths of hundreds of bottlenose dolphins have been tentatively attributed to poisoning from toxins from harmful algal blooms, perhaps through an eosinophilia syndrome (Balmer *et al.*, 2008; Schwacke *et al.*, 2010). The severe and prolonged 2005 *K. brevis* bloom encompassed much of the central and southwest coast of Florida. Elevated levels of mortality of manatees (*Trichechus manatus latirostris*), bottlenose dolphins and marine turtles during this time led to the declaration by US federal agencies of a Multi-species Unusual Mortality Event. While dolphin mortalities involving non-residents increased near Sarasota Bay, none of the long-term resident Sarasota Bay dolphins were found to have died from brevetoxins (Wells, in review). Instead, Sarasota Bay dolphins demonstrated sublethal responses, including emigration of shorter-term residents, and changes in group size, habitat use and social behavior (Wells, in review; McHugh *et al.,* in press). Lagged responses to decreases in prey species availability of 90% or more (Gannon *et al.*, 2009) led to declines in body condition for some vulnerable dolphin age/sex classes, and likely contributed to an increase in lethal interactions with anglers through depredation of bait and catch (Powell and Wells, 2011; Wells *et al.*, 2008). Latent impacts of the red tide are thought to include the deaths in 2006 of 2% of the long-term resident dolphins of Sarasota Bay from ingestion of recreational fishing gear (Powell and Wells, 2011). Increased interactions between anglers and dolphins in the CHPIS area have been noted in recent years. Mortality rates on the order of 2% might not have been detectable through our abundance estimation approach. Such a rate of additional loss, maintained over years, would not be sustainable.

The work reported here provides the necessary information for identifying biologically meaningful bottlenose dolphin management units in the bays, sounds and estuaries of southwestern Florida. The documented long-term stability and site-fidelity in spite of severe natural environmental perturbations pave the way for more detailed studies applying additional tools and information such as genetics, social association patterns, habitat use patterns, stable isotopes and environmental contaminant concentrations to define fine scale stock structure in this region. Long-term studies of well-defined, biologically meaningful population units facilitate potential detection of impacts from a variety of sources, including natural perturbations, human activities including oil spills and climate disruption.

ACKNOWLEDGEMENTS

This project involved many years of dedicated field work and laboratory analyses and would not have been possible without the help of many Sarasota Dolphin Research Program staff and numerous interns and volunteers. We especially thank Bill Carr, Sue Hofmann, Anna Sellas and Gene and Lorry Stover for their multi-year efforts in the field and in the lab. Stephanie Nowacek helped with grading many of the photographs. We thank Dr. Susan Shane for providing her fin catalog and initial sighting year data. We thank Kim Urian and Todd Speakman and two anonymous reviewers for their helpful comments on the manuscript. We greatly appreciate the generosity of Don and Dorothy Gulnac for opening their home to us as a field station on Demere Key after Hurricane Charley destroyed Mote Marine Laboratory's previous field station on Pine Island. Primary support for the multi-year surveys and analyses were provided by Mote Scientific Foundation and the Chicago Zoological Society. Harbor Branch Oceanographic Institute's Protect Wild Dolphins license tag program provided support for the 2006 surveys and some of the analyses to evaluate the effects of Hurricane Charley. Additional support was provided by Mote Marine Laboratory, the National Marine Fisheries Service, Dolphin Biology Research Institute and Earthwatch Institute. Research was conducted under NMFS General Authorization for Scientific Research No. 522-1435 and NMFS Scientific Research Permits No. 522-1569 and No. 522-1785 issued to RSW.

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